

# ESSENTIALS OF ECOLOGY

THIRD EDITION



COLIN R. TOWNSEND, MICHAEL BEGON & JOHN L. HARPER



Blackwell  
Publishing

# ESSENTIALS **OF ECOLOGY**







# ESSENTIALS OF ECOLOGY

Third Edition

## **Colin R. Townsend**

Department of Zoology, University of Otago, Dunedin, New Zealand

## **Michael Begon**

Population Biology Research Group, School of Biological Sciences  
The University of Liverpool, Liverpool, UK

## **John L. Harper**

Professor Emeritus in the University of Wales  
Visiting Professor in the University of Exeter, Exeter, UK

© 2008 by Blackwell Publishing

BLACKWELL PUBLISHING  
350 Main Street, Malden, MA 02148-5020, USA  
9600 Garsington Road, Oxford OX4 2DQ, UK  
550 Swanston Street, Carlton, Victoria 3053, Australia

The right of Colin R. Townsend, Michael Begon, and John L. Harper to be identified as the Authors of this Work has been asserted in accordance with the UK Copyright, Designs, and Patents Act 1988.

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, except as permitted by the UK Copyright, Designs, and Patents Act 1988, without the prior permission of the publisher.

Designations used by companies to distinguish their products are often claimed as trademarks. All brand names and product names used in this book are trade names, service marks, trademarks, or registered trademarks of their respective owners. The publisher is not associated with any product or vendor mentioned in this book.

This publication is designed to provide accurate and authoritative information in regard to the subject matter covered. It is sold on the understanding that the publisher is not engaged in rendering professional services. If professional advice or other expert assistance is required, the services of a competent professional should be sought.

First edition published 2000 by Blackwell Publishing  
Second edition published 2003  
Third edition published 2008

1 2008

*Library of Congress Cataloging-in-Publication Data*

Townsend, Colin R.  
Essentials of ecology / Colin R. Townsend, Michael Begon, John L. Harper.—3rd ed.  
p. cm.  
Includes bibliographical references and index.  
ISBN 978-1-4051-5658-5 (pbk. : alk. paper)  
1. Ecology. I. Begon, Michael. II. Harper, John L. III. Title.  
QH541.T66 2008  
577—dc22 2007034694

A catalogue record for this title is available from the British Library.

Set in 9.5/12pt ClassGarmond  
by Graphicraft Limited, Hong Kong  
Printed and bound in Singapore by C.O.S. Printers Pte Ltd

The publisher's policy is to use permanent paper from mills that operate a sustainable forestry policy, and which has been manufactured from pulp processed using acid-free and elementary chlorine-free practices. Furthermore, the publisher ensures that the text paper and cover board used have met acceptable environmental accreditation standards.

For further information on  
Blackwell Publishing, visit our website:  
[www.blackwellpublishing.com](http://www.blackwellpublishing.com)

# Short contents

## SHORT CONTENTS

*Full contents* vi

*Preface* x

*Acknowledgments* xii

### Part I Introduction 1

- 1 Ecology and how to do it 3
- 2 Ecology's evolutionary backdrop 36

### Part II Conditions and Resources 67

- 3 Physical conditions and the availability of resources 69
- 4 Conditions, resources and the world's communities 110

### Part III Individuals, Populations, Communities and Ecosystems 143

- 5 Birth, death and movement 145
- 6 Interspecific competition 182
- 7 Predation, grazing and disease 217
- 8 Evolutionary ecology 251
- 9 From populations to communities 281
- 10 Patterns in species richness 323
- 11 The flux of energy and matter through ecosystems 357

### Part IV Applied Issues in Ecology 387

- 12 Sustainability 389
- 13 Habitat degradation 423
- 14 Conservation 455

*References* 483

*Index* 495

# CONTENTS

*Preface* x  
*Acknowledgments* xii

## Part I Introduction 1

### 1 Ecology and how to do it 3

- 1.1 Introduction 4
- 1.2 Scales, diversity and rigor 7
- 1.3 Ecology in practice 17

### 2 Ecology's evolutionary backdrop 36

- 2.1 Introduction 37
- 2.2 Evolution by natural selection 37
- 2.3 Evolution within species 41
- 2.4 The ecology of speciation 51
- 2.5 Effects of climatic change on the evolution and distribution of species 58
- 2.6 Effects of continental drift on the ecology of evolution 60
- 2.7 Interpreting the results of evolution: convergents and parallels 63

## Part II Conditions and Resources 67

### 3 Physical conditions and the availability of resources 69

- 3.1 Introduction 70
- 3.2 Environmental conditions 71
- 3.3 Plant resources 84
- 3.4 Animals and their resources 95
- 3.5 Effects of intraspecific competition for resources 103
- 3.6 Conditions, resources and the ecological niche 106

## 4 Conditions, resources and the world's communities 110

- 4.1 Introduction 111
- 4.2 Geographic patterns at large and small scales 111
- 4.3 Temporal patterns in conditions and resources 117
- 4.4 Terrestrial biomes 119
- 4.5 Aquatic environments 130

## Part III Individuals, Populations, Communities and Ecosystems 143

---



## 5 Birth, death and movement 145

- 5.1 Introduction 146
- 5.2 Life cycles 151
- 5.3 Monitoring birth and death: life tables and fecundity schedules 156
- 5.4 Dispersal and migration 164
- 5.5 The impact of intraspecific competition on populations 169
- 5.6 Life history patterns 175

## 6 Interspecific competition 182

- 6.1 Introduction 183
- 6.2 Ecological effects of interspecific competition 183
- 6.3 Evolutionary effects of interspecific competition 197
- 6.4 Interspecific competition and community structure 200
- 6.5 How significant is interspecific competition in practice? 208

## 7 Predation, grazing and disease 217

- 7.1 Introduction 218
- 7.2 Prey fitness and abundance 220
- 7.3 The subtleties of predation 222
- 7.4 Predator behavior: foraging and transmission 228
- 7.5 Population dynamics of predation 233
- 7.6 Predation and community structure 246

## 8 Evolutionary ecology 251

- 8.1 Introduction 252
- 8.2 Molecular ecology: differentiation within and between species 253
- 8.3 Coevolutionary arms races 262
- 8.4 Mutualistic interactions 267

## 9 From populations to communities 281

- 9.1 Introduction 282
- 9.2 Multiple determinants of the dynamics of populations 283
- 9.3 Dispersal, patches and metapopulation dynamics 294
- 9.4 Temporal patterns in community composition 299
- 9.5 Food webs 307

## 10 Patterns in species richness 323

- 10.1 Introduction 324
- 10.2 A simple model of species richness 326
- 10.3 Spatially varying factors that influence species richness 328
- 10.4 Temporally varying factors that influence species richness 337
- 10.5 Gradients of species richness 340
- 10.6 Patterns in taxon richness in the fossil record 349
- 10.7 Appraisal of patterns in species richness 352

## 11 The flux of energy and matter through ecosystems 357

- 11.1 Introduction 358
- 11.2 Primary productivity 360
- 11.3 The fate of primary productivity 364
- 11.4 The process of decomposition 369
- 11.5 The flux of matter through ecosystems 374
- 11.6 Global biogeochemical cycles 380

## Part IV Applied Issues in Ecology 387

### 12 Sustainability 389

- 12.1 Introduction 390
- 12.2 The human population 'problem' 391
- 12.3 Harvesting living resources from the wild 399
- 12.4 The farming of monocultures 405
- 12.5 Pest control 412
- 12.6 Integrated farming systems 417
- 12.7 Forecasting agriculturally driven global environmental change 419

### 13 Habitat degradation 423

- 13.1 Introduction 424
- 13.2 Degradation via cultivation 428
- 13.3 Power generation and its diverse effects 435
- 13.4 Degradation in urban and industrial landscapes 442
- 13.5 Maintenance and restoration of ecosystem services 448



## 14 Conservation 455

14.1 Introduction 456

14.2 Threats to biodiversity 459

14.3 Conservation in practice 468

14.4 Conservation in a changing world 476

14.5 Finale 479

*References* 483

*Index* 495



# Preface

## PREFACE

By writing this book we hope to share with you some of our wonder at the complexity of nature, but we must all also be aware that there is a darker side: the fear that we are destroying our natural environments and the services they provide. All of us need to be ecologically literate so that we can take part in political debate and contribute to solving the ecological problems that we carry with us into the new millennium. We hope our book will contribute to this objective.

The genesis of this book can be found in the more comprehensive treatment of ecology in our big book *Ecology: from Individuals to Ecosystems* (Begon, Townsend & Harper, 4th edn, 2006). This is used as an advanced university text around the world, but many of our colleagues have called for a more succinct treatment of the essence of the subject. Thus, we were spurred into action to produce a distinctively different book, written with clear objectives for a different audience – those taking a semester-long beginners course in the essentials of ecology. We hope that at least some readers will be excited enough to go on to sample the big book and the rich literature of ecology that it can lead into.

In this third edition of *Essentials of Ecology* we have made the text, including mathematical topics, even more accessible. Ecology is a vibrant subject and this is reflected by our inclusion of literally hundreds of new studies. Some readers will be engaged most by the fundamental principles of how ecological systems work. Others will be impatient to focus on the ecological problems caused by human activities. We place heavy emphasis on both fundamental and applied aspects of ecology: there is no clear boundary between the two. However, we have chosen to deal first in a systematic way with the fundamental side of the subject, and we have done this for a particular reason. An understanding of the scope of the problems facing us (the unsustainable use of ecological resources, pollution, extinctions and the erosion of natural biodiversity) and the means to counter and solve these problems depend absolutely on a proper grasp of ecological fundamentals.

The book is divided into four sections. In the introduction we deal with two foundations for the subject that are often neglected in texts. Chapter 1 aims to show not only what ecology is but also how ecologists do it – how ecological understanding is achieved, what we understand (and, just as important, what we do not yet understand) and how our understanding helps us predict and manage. We then introduce ‘Ecology’s evolutionary backdrop’ and show that ecologists need a full understanding of the evolutionary biologist’s discipline in order to make sense of patterns and processes in nature (Chapter 2).

What makes an environment habitable for particular species is that they can tolerate the physicochemical conditions there and find in it their essential resources.

In the second section we deal with conditions and resources, both as they influence individual species (Chapter 3) and in terms of their consequences for the composition and distribution of multispecies communities, for example in deserts, rain forests, rivers, lakes and oceans (Chapter 4).

The third section (Chapters 5–11) deals systematically with the ecology of individual organisms, populations of a single species, communities consisting of many populations, and ecosystems (where we focus on the fluxes of energy and matter between and within communities). To understand patterns and processes at each of these levels we need to know the behavior of the level below. This section also includes a new Chapter 8 on ‘Evolutionary ecology’, responding to the feelings of some readers that, although evolutionary ideas pervade the book, there was still not sufficient evolution for a book at this level.

Finally, armed with knowledge and understanding of the fundamentals, the book turns to the applied questions of how to deal with pests and manage resources sustainably (whether wild populations of fish or agricultural monocultures) (Chapter 12), then to a diversity of pollution problems ranging from local enrichment of a lake by sewage to global climate change associated with the use of fossil fuels (Chapter 13) and lastly we develop an armory of approaches that may help us to save endangered species from extinction and conserve some of the biodiversity of nature for our descendants (Chapter 14).

A number of pedagogical features have been included to help you.

- Each chapter begins with a set of key concepts that you should understand before proceeding to the next chapter.
- Marginal headings provide signposts of where you are on your journey through each chapter – these will also be useful revision aids.
- Each chapter concludes with a summary and a set of review questions, some of which are designated challenge questions.
- You will also find three categories of boxed text:
  - ‘Historical landmarks’ boxes emphasize some landmarks in the development of ecology.
  - ‘Quantitative aspects’ boxes set aside mathematical and quantitative aspects of ecology so they do not unduly interfere with the flow of the text and so you can consider them at leisure.
  - ‘Topical ECOncerns’ boxes highlight some of the applied problems in ecology, particularly those where there is a social or political dimension (as there often is). In these, you will be challenged to consider some ethical questions related to the knowledge you are gaining.

An important further feature of the book is the companion internet web site, e.cology, accessed through [www.blackwellpublishing.com](http://www.blackwellpublishing.com) and linked to the companion site of our big book, *Ecology*. This provides an easy-to-use range of resources to aid study and enhance the content of the book. Features include self-assessment multiple choice questions for each chapter in the book, an interactive tutorial to help students to understand the use of mathematical modeling in ecology, and high-quality images of the figures in the book that teachers can use in preparing their lectures or lessons.

# Acknowledgments

## ACKNOWLEDGMENTS

It is a pleasure to record our gratitude to the people who helped with the planning and writing of this book. Going back to the first edition, we thank Bob Campbell and Simon Rallison for getting the original enterprise off the ground and Nancy Whilton and Irene Herlihy for ably managing the project; and for the second edition, Nathan Brown (Blackwell, US) and Rosie Hayden (Blackwell, UK) for making it so easy for us to take this book from manuscript into print. For this third edition, we especially thank Nancy Whilton and Elizabeth Frank in Boston for persuading us to pick up our pens again (not literally) and Rosie Hayden, again, and Jane Andrew and Ward Cooper for seeing us through production. We are also grateful to the following colleagues who provided insightful reviews of early drafts of one or more chapters. For the first edition, Tim Mousseau (University of South Carolina), Vickie Backus (Middlebury College), Kevin Dixon (Arizona State University, West), James Maki (Marquette University), George Middendorf (Howard University), William Ambrose (Bates College), Don Hall (Michigan State University), Clayton Penniman (Central Connecticut State University), David Tonkyn (Clemson University), Sara Lindsay (Scripps Institute of Oceanography), Saran Twombly (University of Rhode Island), Katie O'Reilly (University of Portland), Catherine Toft (UC Davis), Bruce Grant (Widener University), Mark Davis (Macalester College), Paul Mitchell (Staffordshire University, UK) and William Kirk (Keele University, UK); and for the second, James Cahill (University of Alberta), Liane Cochrane-Stafira (Saint Xavier University), Hans deKroon (University of Nijmegen), Jake Weltzin (University of Tennessee at Knoxville) and Alan Wilmot (University of Derby, UK).


For this edition, our long-time mentor and collaborator John Harper has stepped from the treadmill to more fully enjoy his retirement. We owe him a special debt of gratitude that extends far beyond the past co-authorship of this book into all aspects of our lives as ecologists.

Last, and perhaps most, we are glad to thank our wives and families for continuing to support us, listen to us, and ignore us, precisely as required – thanks to Laurel, Dominic, Jenny, Brennan and Amelie, and to Linda, Jessi and Rob.

The publisher would like to thank Denis Saunders, from CSIRO, for use of the image in part 4 of the book.

# PART ONE

## Introduction

- 
- 1 | Ecology and how to do it 3
  - 2 | Ecology's evolutionary backdrop 36



# Chapter 1



## Ecology and how to do it

### *Chapter contents*

#### CHAPTER CONTENTS

- 1.1 Introduction
- 1.2 Scales, diversity and rigor
- 1.3 Ecology in practice

### *Key concepts*

#### KEY CONCEPTS

In this chapter you will:

- learn how to define ecology and appreciate its development as both an applied and a pure science
- recognize that ecologists seek to describe and understand, and on the basis of their understanding, to predict, manage and control
- appreciate that ecological phenomena occur on a variety of spatial and temporal scales, and that patterns may be evident only at particular scales
- recognize that ecological evidence and understanding can be obtained by means of observations, field and laboratory experiments, and mathematical models
- understand that ecology relies on truly scientific evidence (and the application of statistics)

*Nowadays, ecology is a subject about which almost everyone has heard and most people consider to be important – even when they are unsure about the exact meaning of the term. There can be no doubt that it is important; but this makes it all the more critical that we understand what it is and how to do it.*

## 1.1 Introduction

the earliest ecologists

The question ‘What is ecology?’ could be translated into ‘How do we define ecology?’ and answered by examining various definitions of ecology that have been proposed and choosing one of them as the best (Box 1.1). But while definitions have conciseness and precision, and they are good at preparing you for an examination, they



## 1.1 Historical landmarks

### Definitions of ecology

Ecology (originally in German, *Ökologie*) was first defined in 1866 by Ernst Haeckel, an enthusiastic and influential disciple of Charles Darwin. To him, ecology was ‘the comprehensive science of the relationship of the organism to the environment’. The spirit of this definition is very clear in an early discussion of biological subdisciplines by Burdon-Sanderson (1893), in which ecology is ‘the science which concerns itself with the external relations of plants and animals to each other and to the past and present conditions of their existence’, to be contrasted with physiology (internal relations) and morphology (structure). For many, such definitions have stood the test of time. Thus, Ricklefs (1973) in his textbook defined ecology as ‘the study of the natural environment, particularly the interrelationships between organisms and their surroundings’.

In the years after Haeckel, plant ecology and animal ecology drifted apart. Influential works defined ecology as ‘those relations of *plants*, with their surroundings and with one another, which depend directly upon differences of habitat among plants’ (Tansley, 1904), or as the science ‘chiefly concerned with what may be called the sociology and economics of *animals*,

rather than with the structural and other adaptations possessed by them’ (Elton, 1927). The botanists and zoologists, though, have long since agreed that they belong together and that their differences must be reconciled.

There is, nonetheless, something disturbingly vague about the many definitions of ecology that seem to suggest that it consists of all those aspects of biology that are neither physiology nor morphology. In search of more focus, therefore, Andrewartha (1961) defined ecology as ‘the scientific study of the distribution and abundance of organisms’, and Krebs (1972), regretting that the central role of ‘relationships’ had been lost, modified it to ‘the scientific study of the *interactions* that determine the distribution and abundance of organisms’, explaining that ecology was concerned with ‘*where* organisms are found, *how many* occur there, and *why*’. This being so, it might be better still to define ecology as:

the scientific study of the distribution and abundance of organisms and the interactions that determine distribution and abundance.



are not so good at capturing the flavor, the interest or the excitement of ecology. There is a lot to be gained by replacing that single question about definition with a series of more provoking ones: ‘What do ecologists *do*?’, ‘What are ecologists *interested in*?’ and ‘Where did ecology emerge from in the first place?’

Ecology can lay claim to be the oldest science. If, as our preferred definition has it, ‘Ecology is the scientific study of the distribution and abundance of organisms and the interactions that determine distribution and abundance’ (Box 1.1), then the most primitive humans must have been ecologists of sorts – driven by the need to understand where and when their food and their (non-human) enemies were to be found – and the earliest agriculturalists needed to be even more sophisticated: having to know how to manage their living but domesticated sources of food. These early ecologists, then, were *applied* ecologists, seeking to understand the distribution and abundance of organisms in order to apply that knowledge for their own collective benefit. They were interested in many of the sorts of things that applied ecologists are still interested in: how to maximize the rate at which food is collected from natural environments, and how this can be done repeatedly over time; how domesticated plants and animals can best be planted or stocked so as to maximize rates of return; how food organisms can be protected from their own natural enemies; and how to control the populations of pathogens and parasites that live on us.

In the last century or so, however, since ecologists have been self-conscious enough to give themselves a name, ecology has consistently covered not only applied but also fundamental, ‘pure’ science. A.G. Tansley was one of the founding fathers of ecology. He was concerned especially to understand, for understanding’s sake, the processes responsible for determining the structure and composition of different plant communities. When, in 1904, he wrote from Britain about ‘The problems of ecology’ he was particularly worried by a tendency for too much ecology to remain at the descriptive and unsystematic stage (i.e. accumulating descriptions of communities without knowing whether they were typical, temporary or whatever), too rarely moving on to experimental or systematically planned, or what we might call a ‘scientific’, analysis.

His worries were echoed in the United States by another of ecology’s founders, F.E. Clements, who in 1905 in his *Research Methods in Ecology* complained:

The bane of the recent development popularly known as ecology has been a widespread feeling that anyone can do ecological work, regardless of preparation. There is nothing . . . more erroneous than this feeling.

On the other hand, the need of *applied* ecology to be based on its *pure* counterpart was clear in the introduction to Charles Elton’s (1927) *Animal Ecology* (Figure 1.1):

Ecology is destined for a great future . . . The tropical entomologist or mycologist or weed-controller will only be fulfilling his functions properly if he is first and foremost an ecologist.

In the intervening years, the coexistence of these pure and applied threads has been maintained and built upon. Many applied areas have contributed to the development of ecology and have seen their own development enhanced by ecological ideas and approaches. All aspects of food and fiber gathering, production and protection have been involved: plant ecophysiology, soil maintenance, forestry, grassland composition and management, food storage, fisheries, and control of pests and pathogens. Each of these classic areas is still at the forefront of

a pure and applied science



### Figure 1.1

One of the great founders of ecology: Charles Elton (1900–1991). *Animal Ecology* (1927) was his first book but *The Ecology of Invasions by Animals and Plants* (1958) was equally influential.



lots of good ecology and they have been joined by others. The biological control of pests (the use of pests' natural enemies to control them) has a history going back at least to the Ancient Chinese but has seen a resurgence of ecological interest since the shortcomings of chemical pesticides began to be widely apparent in the 1950s. The ecology of pollution has been a growing concern from around the same time and expanded further in the 1980s and 1990s from local to global issues. The closing decades of the last millennium also saw expansions both in public interest and ecological input into the conservation of endangered species and the biodiversity of whole areas, in the control of disease in humans as well as many other species, and in the potential consequences of profound human-caused changes to the global environment.

#### unanswered questions

And yet, at the same time, many fundamental problems of ecology remain unanswered. To what extent does competition for food determine which species can coexist in a habitat? What role does disease play in the dynamics of populations? Why are there more species in the tropics than at the poles? What is the relationship between soil productivity and plant community structure? Why are some species more vulnerable to extinction than others? And so on. Of course, unanswered questions – if they are *focused* questions – are a symptom of the health not the weakness of any science. But ecology is not an easy science, and it has particular subtlety and complexity, in part because ecology is peculiarly confronted by 'uniqueness': millions of different species, countless billions of genetically distinct individuals, all living and interacting in a varied and ever-changing world. The beauty of ecology is that it challenges us to develop an understanding of very basic and apparent problems – in a way that recognizes the uniqueness and complexity of all aspects of nature – but seeks patterns and predictions within this complexity rather than being swamped by it.

Summarizing this brief historical overview, it is clear that ecologists try to do a number of different things. First and foremost ecology is a science, and ecologists therefore try to *explain* and *understand*. There are two different classes of explanation in biology: ‘proximate’ and ‘ultimate’. For example, the present distribution and abundance of a particular species of bird may be ‘explained’ in terms of the physical environment that the bird tolerates, the food that it eats and the parasites and predators that attack it. This is a *proximate* explanation – an explanation in terms of what is going on ‘here and now’. However, we can also ask how this bird has come to have these properties that now govern its life. This question has to be answered by an explanation in evolutionary terms; the *ultimate* explanation of the present distribution and abundance of this bird lies in the ecological experiences of its ancestors (see Chapter 2).

In order to understand something, of course, we must first have a description of whatever it is we wish to understand. Ecologists must therefore *describe* before they explain. On the other hand, the most valuable descriptions are those carried out with a particular problem or ‘need for understanding’ in mind. Undirected description, carried out merely for its own sake, is often found afterwards to have selected the wrong things and has little place in ecology – or any other science.

Ecologists also often try to *predict* what will happen to a population of organisms under a particular set of circumstances, and on the basis of these predictions to control, exploit or conserve the population. We try to minimize the effects of locust plagues by predicting when they are likely to occur and taking appropriate action. We try to exploit crops most effectively by predicting when conditions will be favorable to the crop and unfavorable to its enemies. We try to preserve rare species by predicting the conservation policy that will enable us to do so. Some prediction and control can be carried out without deep explanation or understanding: it is not difficult to predict that the destruction of a woodland will eliminate woodland birds. But insightful predictions, precise predictions and predictions of what will happen in unusual circumstances can be made only when we can also explain and understand what is going on.

This book is therefore about:

- 1 How ecological understanding is achieved.
- 2 What we do understand (but also what we do not understand).
- 3 How that understanding can help us predict, manage and control.

## 1.2 Scales, diversity and rigor

The rest of this chapter is about the two ‘hows’ above: how understanding is achieved, and how that understanding can help us predict, manage and control. Later in the chapter we illustrate three fundamental points about doing ecology by examining a limited number of examples in some detail (Section 1.3). But first we elaborate on the three points, namely:

- ecological phenomena occur at a variety of scales;
- ecological evidence comes from a variety of different sources;
- ecology relies on truly scientific evidence and the application of statistics.

### 1.2.1 Questions of scale

Ecology operates at a range of scales: time scales, spatial scales and ‘biological’ scales. It is important to appreciate the breadth of these and how they relate to one another.

the ‘biological’ scale

The living world is often said to comprise a biological hierarchy beginning with subcellular particles and continuing through cells, tissues and organs. Ecology then deals with the next three levels:

- *individual organisms*;
- *populations* (consisting of individuals of the same species);
- *communities* (consisting of a greater or lesser number of populations).

At the level of the organism, ecology deals with how individuals are affected by (and how they affect) their environment. At the level of the population, ecology deals with the presence or absence of particular species, with their abundance or rarity, and with the trends and fluctuations in their numbers. Community ecology then deals with the composition or structure of ecological communities.

We can also focus on the pathways followed by energy and matter as these move among living and non-living elements of a fourth category of organization:

- *ecosystems* (comprising the community together with its physical environment).

With this level of organization in mind, Likens (1992) would extend our preferred definition of ecology (Box 1.1) to include ‘the interactions between organisms and the transformation and flux of energy and matter’. However, we take energy/matter transformations as being subsumed in the ‘interactions’ of our definition.

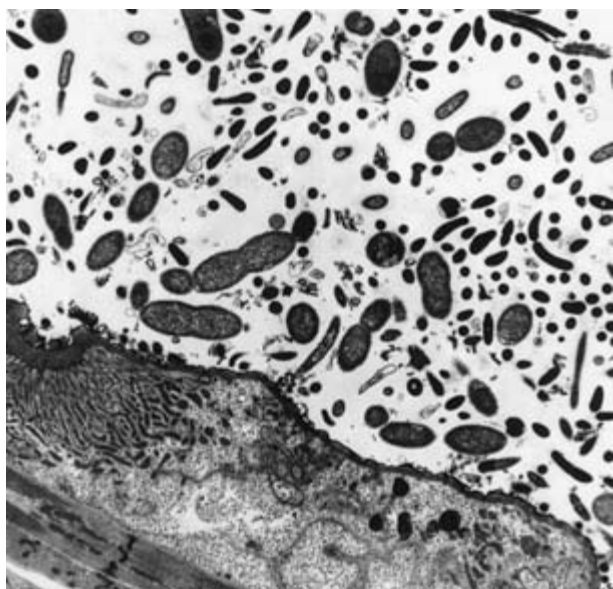
a range of spatial scales

Within the living world, there is no arena too small nor one so large that it does not have an ecology. Even the popular press talk increasingly about the ‘global ecosystem’ and there is no question that several ecological problems can only be examined at this very large scale. These include the relationships between ocean currents and fisheries, or between climate patterns and the distribution of deserts and tropical rain forests, or between elevated carbon dioxide in the atmosphere (from burning fossil fuels) and global climate change.

At the opposite extreme, an individual cell may be the stage on which two populations of pathogens compete with one another for the resources that the cell provides. At a slightly larger spatial scale, a termite’s gut is the habitat for bacteria, protozoans and other species (Figure 1.2) – a community whose diversity is comparable to that of a tropical rain forest in terms of the richness of organisms living there, the variety of interactions in which they take part, and indeed the extent to which we remain ignorant about the species identity of many of the participants. Between these extremes, different ecologists, or the same ecologist at different times, may study the inhabitants of pools that form in small tree-holes, the temporary watering holes of the savannas, or the great lakes and oceans; others may examine the diversity of fleas on different species of birds, the diversity of birds in different sized patches of woodland, or the diversity of woodlands at different altitudes.

a range of time scales

To some extent related to this range of spatial scales, and to the levels in the biological hierarchy, ecologists also work on a variety of time scales. ‘Ecological succession’ – the successive and continuous colonization of a site by certain species populations, accompanied by the extinction of others – may be studied over a period from the deposition of a lump of sheep dung to its decomposition (a

**Figure 1.2**

The diverse community of a termite's gut. Termites can break down lignin and cellulose from wood because of their mutualistic relationships (see Section 8.4.4) with a diversity of microbes that live in their guts.

matter of weeks), or from the change in climate at the end of the last ice age to the present day and beyond (around 14,000 years and still counting). Migration may be studied in butterflies over the course of days, or in the forest trees that are still (slowly) migrating into deglaciated areas following that last ice age.

Although it is undoubtedly the case that ‘appropriate’ time scales vary, it is also true that many ecological studies are not as long as they might be. Longer studies cost more and require greater dedication and stamina. An impatient scientific community, and the requirement for concrete evidence of activity for career progression, both put pressure on ecologists, and all scientists, to publish their work sooner rather than later. Why are long-term studies potentially of such value? The reduction over a few years in the numbers of a particular species of wild flower, or bird, or butterfly might be a cause for conservation concern – but one or more decades of study may be needed to be sure that the decline is more than just an expression of the random ups and downs of ‘normal’ population dynamics. Similarly, a 2-year rise in the abundance of a wild rodent followed by a 2-year fall might be part of a regular ‘cycle’ in abundance, crying out for an explanation. But ecologists could not be sure until perhaps 20 years of study has allowed them to record four or five repeats of such a cycle.

This does not mean that all ecological studies need to last for 20 years – nor that every time an ecological study is extended the answer changes. But it does emphasize the great value to ecology of the small number of long-term investigations that have been carried out or are ongoing.

the need for long-term studies

### 1.2.2 The diversity of ecological evidence

Ecological evidence comes from a variety of different sources. Ultimately, ecologists are interested in organisms in their natural environments (though for many organisms, the environment which is ‘natural’ for them now is itself manmade). Progress would be impossible, however, if ecological studies were limited to such

## observations and field experiments

natural environments. And, even in natural habitats, unnatural acts (experimental manipulations) are often necessary in the search for sound evidence.

Many ecological studies involve careful *observation* and monitoring, in the natural environment, of the changing abundance of one or more species over time, or over space, or both. In this way, ecologists may establish patterns; for example, that red grouse (birds shot for ‘sport’) exhibit regular cycles in abundance peaking every 4 or 5 years, or that vegetation can be mapped into a series of zones as we move across a landscape of sand dunes. But scientists do not stop at this point – the patterns require explanation. Careful analysis of the descriptive data may suggest some plausible explanations. But establishing what causes the patterns may well require *manipulative field experiments*: ridding the red grouse of intestinal worms, hypothesized to underlie the cycles, and checking if the cycles persist (they do not: Hudson et al., 1998), or treating experimental areas on sand dunes with fertilizer to see whether the changing pattern of vegetation itself reflects a changing pattern of soil productivity.

## laboratory experiments

Perhaps less obviously, ecologists also often need to turn to laboratory systems and even mathematical models. These have played a crucial role in the development of ecology, and they are certain to continue to do so. Field experiments are almost inevitably costly and difficult to carry out. Moreover, even if time and expense were not issues, natural field systems may simply be too complex to allow us to tease apart the consequences of the many different processes that may be going on. Are the intestinal worms actually capable of having an effect on reproduction or mortality of individual grouse? Which of the many species of sand dune plants are, in themselves, sensitive to changing levels of soil productivity and which are relatively insensitive? *Controlled, laboratory experiments* are often the best way to provide answers to specific questions that are key parts of an overall explanation of the complex situation in the field.

## simple laboratory systems . . .

Of course, the complexity of natural ecological communities may simply make it inappropriate for an ecologist to dive straight into them in search of understanding. We may wish to explain the structure and dynamics of a particular community of 20 animal and plant species comprising various competitors, predators, parasites and so on (relatively speaking, a community of remarkable simplicity). But we have little hope of doing so unless we already have some basic understanding of even simpler communities of just one predator and one prey species, or two competitors, or (especially ambitious) two competitors that also share a common predator. For this, it is usually most appropriate to construct, for our own convenience, *simple laboratory systems* that can act as benchmarks or jumping-off points in our search for understanding.

## . . . and mathematical models

What is more, you have only to ask anyone who has tried to rear caterpillar eggs, or take a cohort of shrub cuttings through to maturity, to discover that even the simplest ecological communities may not be easy to maintain or keep free of unwanted pathogens, predators or competitors. Nor is it necessarily possible to construct precisely the particular, simple, artificial community that interests you; nor to subject it to precisely the conditions or the perturbation of interest. In many cases, therefore, there is much to be gained from the analysis of *mathematical models* of ecological communities: constructed and manipulated according to the ecologist’s design.

On the other hand, although a major aim of science is to simplify, and thereby make it easier to understand the complexity of the real world, ultimately it is the

real world that we are interested in. The worth of models and simple laboratory experiments must always be judged in terms of the light they throw on the working of more natural systems. They are a means to an end – never an end in themselves. Like all scientists, ecologists need to ‘seek simplicity, but distrust it’ (Whitehead, 1953).

### 1.2.3 Statistics and scientific rigor

For a scientist to take offence at some popular phrase or saying is to invite accusations of a lack of a sense of humor. But it is difficult to remain calm when phrases like ‘There are lies, damn lies and statistics’ or ‘You can prove anything with statistics’ are used, by those who should know better, to justify continuing to believe what they wish to believe, whatever the evidence to the contrary. There is no doubt that statistics are sometimes *mis*-used to derive dubious conclusions from sets of data that actually suggest either something quite different or perhaps nothing at all. But these are not grounds for mistrusting statistics in general – rather for ensuring that people are educated in at least the principles of scientific evidence and its statistical analysis, so as to protect them from those who may seek to manipulate their opinions.

In fact, not only is it not true that you can prove anything with statistics, the contrary is the case: you cannot *prove* anything with statistics – that is not what statistics are for. Statistical analysis is essential, however, for attaching a level of confidence to conclusions that can be drawn; and ecology, like all science, is a search not for statements that have been ‘proved to be true’ but for conclusions in which we can be confident.

Indeed, what distinguishes science from other activities – what makes science ‘rigorous’ – is that it is based not on statements that are simply assertions, but that it is based (i) on conclusions that are the results of investigations (as we have seen, of a wide variety of types) carried out with the express purpose of deriving those conclusions; and (b) even more important, on conclusions to which a level of confidence can be attached, measured on an agreed scale. These points are elaborated in Boxes 1.2 and 1.3.

Statistical analyses are carried out after data have been collected, and they help us to interpret those data. There is no really good science, however, without forethought. Ecologists, like all scientists, must know what they are doing, and why they are doing it, *while* they are doing it. This is entirely obvious at a general level: nobody expects ecologists to be going about their work in some kind of daze. But it is perhaps not so obvious that ecologists should know how they are going to analyze their data, statistically, not only after they have collected it, not only while they are collecting it, but even before they begin to collect it. Ecologists must plan, so as to be confident that they have collected the right kind of data, and a sufficient amount of data, to address the questions they hope to answer.

Ecologists typically seek to draw conclusions about groups of organisms overall: what is the birth rate of the bears in Yellowstone Park? What is the density of weeds in a wheat field? What is the rate of nitrogen uptake of tree saplings in a nursery? In doing so, we can only very rarely examine every individual in a group, or in the entire sampling area, and we must therefore rely on what we hope will be a *representative* sample from the group or habitat. Indeed, even if we examined a whole group (we might examine every fish in a small pond, say),

ecology: a search for conclusions in which we can be confident

ecologists must think ahead

ecology relies on representative samples





## 1.2 Quantitative aspects

### 1.2 QUANTITATIVE ASPECTS

#### Interpreting probabilities

##### **P-values**

The term that is most often used, at the end of a statistical test, to measure the strength of conclusions being drawn is a *P*-value, or probability level. It is important to understand what *P*-values are. Imagine we are interested in establishing whether high abundances of a pest insect in summer are associated with high temperatures the previous spring, and imagine that the data we have to address this question consist of summer insect abundances and mean spring temperatures for each of a number of years. We may reasonably hope that statistical analysis of our data will allow us either to conclude, with a stated degree of confidence, that there is an association, or to conclude that there are no grounds for believing there to be an association (Figure 1.3).

##### **Null hypotheses**

To carry out a statistical test we first need a *null hypothesis*, which simply means, in this case, that there is *no* association: that is, no association between insect abundance and temperature. The statistical test (stated simply) then generates a probability (a *P*-value) of getting a data set like ours if the null hypothesis is correct.

Suppose the data were like those in Figure 1.3a. The probability generated by a test of association on these data is  $P = 0.5$  (equivalently 50%). This means that, if the null hypothesis really was correct (no association), then 50% of studies like ours should generate just such a data set, or one even further from the null hypothesis. So, if there was no association, there would be nothing very remarkable in this data set, and we could have no confidence in any claim that there was an association.

Suppose, however, that the data were like those in Figure 1.3b, where the *P*-value generated is  $P = 0.001$  (0.1%). This would mean that such a data set (or one even further from the null hypothesis) could be expected in only 0.1% of similar studies if there was really no association. In other words, either something

very improbable has occurred, or there was an association between insect abundance and spring temperature. Thus, since by definition we do not expect highly improbable events to occur, we can have a high degree of confidence in the claim that there was an association between abundance and temperature.

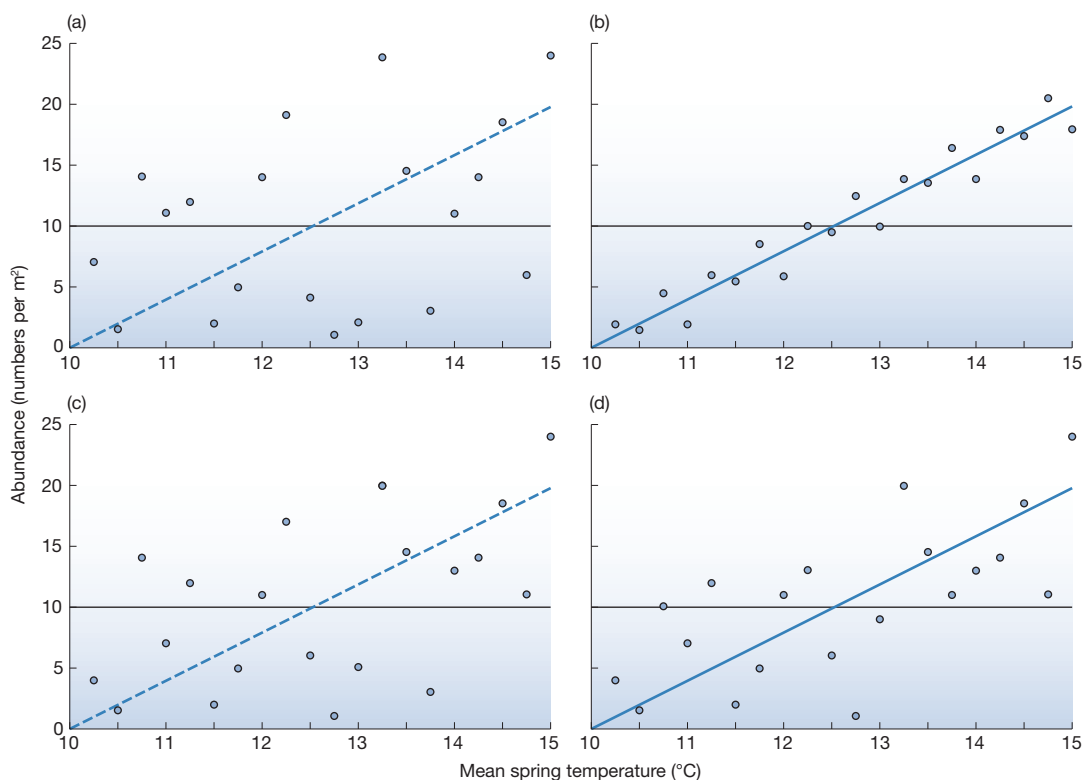
##### **Significance testing**

Both 50% and 0.01%, though, make things easy for us. Where, between the two, do we draw the line? There is no objective answer to this, and so scientists and statisticians have established a convention in *significance testing*, which says that if *P* is less than 0.05 (5%), written  $P < 0.05$  (e.g. Figure 1.3d), then results are described as statistically significant and confidence can be placed in the effect being examined (in our case, the association between abundance and temperature), whereas if  $P > 0.05$ , then there is no statistical foundation for claiming the effect exists (e.g. Figure 1.3c). A further elaboration of the convention often describes results with  $P < 0.01$  as 'highly significant'.

##### **'Insignificant' results?**

Naturally, some effects are strong (for example, there is a powerful association between people's weight and their height) and others are weak (the association between people's weight and their risk of heart disease is real but weak, since weight is only one of many important factors). More data are needed to establish support for a weak effect than for a strong one. A rather obvious but very important conclusion follows from this: a *P*-value in an ecological study of greater than 0.05 (lack of statistical significance) may mean one of two things:

- 1 There really is no effect of ecological importance.
- 2 The data are simply not good enough, or there are not enough of them, to support the effect even though it exists, possibly because the effect itself is real but weak, and extensive data are therefore needed but have not been collected.



**Figure 1.3**

The results from four hypothetical studies of the relationship between insect pest abundance in summer and mean temperature the previous spring. In each case, the points are the data actually collected. Horizontal lines represent the *null hypothesis* – that there is no association between abundance and temperature, and thus the best estimate of expected insect abundance, irrespective of spring temperature, is the mean insect abundance overall. The second line is the *line of best fit* to the data, which in each case offers some suggestion that abundance rises as temperature rises. However, whether we can be confident in concluding that abundance does rise with temperature depends, as explained in the text, on statistical tests applied to the data sets. (a) The suggestion of a relationship is weak ( $P = 0.5$ ). There are no good grounds for concluding that the true relationship differs from that supposed by the null hypothesis and no grounds for concluding that abundance is related to temperature. (b) The relationship is strong ( $P = 0.001$ ) and we can be confident in concluding that abundance increases with temperature. (c) The results are suggestive ( $P = 0.1$ ) but it would not be safe to conclude from them that abundance rises with temperature. (d) The results are not vastly different from those in (c) but are powerful enough ( $P = 0.04$ , i.e.  $P < 0.05$ ) for the conclusion that abundance rises with temperature to be considered safe.

### Quoting *P*-values

Furthermore, applying the convention strictly and dogmatically means that when  $P = 0.06$  the conclusion should be ‘no effect has been established’, whereas when  $P = 0.04$  the conclusion is ‘there is a significant effect’. Yet very little difference in the data is required to move a  $P$ -value from 0.04 to 0.06. It is therefore far better to quote exact  $P$ -values, especially when they exceed 0.05, and think of conclusions in terms of

shades of gray rather than the black and white of ‘proven effect’ and ‘no effect’. In particular,  $P$ -values close to, but not less than, 0.05 suggest that something seems to be going on; they indicate, more than anything else, that more data need to be collected so that our confidence in conclusions can be more clearly established.

Throughout this book, then, studies of a wide range of types are described, and their results often



have  $P$ -values attached to them. Of course, as this is a textbook, the studies have been selected because their results *are* significant. Nonetheless, it is important to bear in mind that the repeated statements  $P < 0.05$  and  $P < 0.01$  mean that these are studies

where: (i) sufficient data have been collected to establish a conclusion in which we can be confident; (ii) that confidence has been established by agreed means (statistical testing); and (iii) confidence is being measured on an agreed and interpretable scale.



## 1.3 Quantitative aspects

### Attaching confidence to results

#### Standard errors and confidence intervals

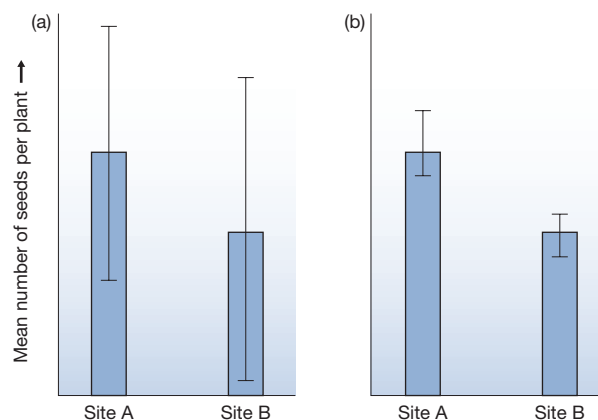
Following Box 1.2, another way in which the significance of results, and confidence in them, is assessed is through reference to standard errors. Again, simply stated, statistical tests often allow standard errors to be attached either to mean values calculated from a set of observations or to slopes of lines like those in Figure 1.3. Such mean values or slopes can, at best, only ever be estimates of the 'true' mean value or true slope, because they are calculated from data that are only a sample of all the imaginable items of data that could be collected. The standard error, then, sets a band around the estimated mean (or slope, etc.) within which the true mean can be expected to lie with a given, stated probability. In particular, there is a 95% probability that the true mean lies within roughly

two standard errors (2 SE) of the estimated mean; we call this the *95% confidence interval*.

Hence, when we have, say, two sets of observations, each with its own mean value (for instance, the number of seeds produced by plants from two sites, Figure 1.4) the standard errors allow us to assess whether the means are significantly different from one another, statistically. Roughly speaking, if each mean is more than two standard errors from the other mean, then the difference between them is statistically significant with  $P < 0.05$ . Thus, for the study illustrated in Figure 1.4a, it would not be safe to conclude that plants from the two sites differed in their seed production. However, for the similar study illustrated in Figure 1.4b, the means are roughly the same as they were in the first study and are roughly as far apart, but the standard errors

**Figure 1.4**

The results of two hypothetical studies in which the seed production of plants from two different sites was compared. In all cases, the heights of the bars represent the mean seed production of the sample of plants examined, and the lines crossing those means extend 1 SE above and below them. (a) Although the means differ, the standard errors are relatively large and it would not be safe to conclude that seed production differed between the sites ( $P = 0.4$ ). (b) The differences between the means are very similar to those in (a), but the standard errors are much smaller, and it can be concluded with confidence that plants from the two sites differed in their seed production ( $P < 0.05$ ).



are smaller. Hence, the difference between the means is significant ( $P < 0.05$ ), and we can conclude with confidence that plants from the two sites differed.

#### When are standard errors small?

Note that the large standard errors in the first study, and hence the lack of statistical significance, could

have been due to data that were, for whatever reason, more variable; but they may also have been due to sampling fewer plants in the first study than the second. Standard errors are smaller, and statistical significance is easier to achieve, *both* when data are more consistent (less variable) *and* when there are more data.

we are likely to want to draw general conclusions from it: we might hope that the fish in 'our' pond can tell us something about fish of that species in ponds of that type, generally. In short, ecology relies on obtaining *estimates* from representative samples. This is elaborated in Box 1.4.



## 1.4 Quantitative aspects

### Estimation: sampling, accuracy and precision

The discussion in Boxes 1.2 and 1.3 about when standard errors will be small or large, or when our confidence in conclusions will be strong or weak, not only has implications for the interpretation of data after they have been collected, but also carries a general message about planning the collection of data. In undertaking a sampling program to collect data, the aim is to satisfy a number of criteria:

- 1 That the estimate should be accurate or unbiased: that is, neither systematically too high nor too low as a result of some flaw in the program.
- 2 That the estimate should have as narrow confidence limits (be as precise) as possible.
- 3 That the time, money and human effort invested in the program should be used as effectively as possible (because these are always limited).

#### Random and stratified random sampling

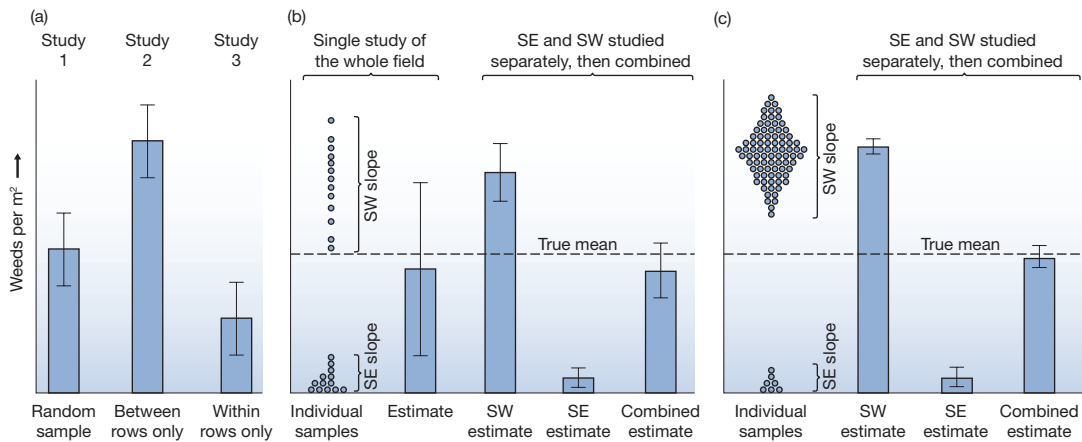
To understand these criteria, consider another hypothetical example. Suppose that we are interested in the density of a particular weed (say wild oat) in a wheat field. To prevent bias, it is necessary to ensure that each part of the field has an equal chance of being selected for sampling. Sampling units should

therefore be selected at random. We might, for example, divide the field into a measured grid, pick points on the grid at random, and count the wild oat plants within a 50 cm radius of the selected grid point. This unbiased method can be contrasted with a plan to sample only weeds from between the rows of wheat plants, giving too high an estimate, or within the rows, giving too low an estimate (Figure 1.5a).

Remember, however, that random samples are not taken as an end in themselves, but because random sampling is a means to truly representative sampling. Thus, randomly chosen sampling units may end up being concentrated, by chance, in a particular part of the field that, unknown to us, is not representative of the field as a whole. It is often preferable, therefore, to undertake *stratified random sampling* in which, in this case, the field is divided up into a number of equal-sized parts (*strata*) and a random sample taken from each. This way, the coverage of the whole field is more even, without our having introduced bias by selecting particular spots for sampling.

#### Separating subgroups and directing effort

Suppose now, though, that half the field is on a slope facing southeast and the other half on a slope facing



**Figure 1.5**

The results of hypothetical programs to estimate weed density in a wheat field. (a) The three studies have equal precision (95% confidence intervals) but only the first (from a random sample) is accurate. (b) In the first study, individual samples from different parts of the field (southeast and southwest) fall into two groups (left); thus, the estimate, although accurate, is not precise (right). In the second study, separate estimates for southeast and southwest are both accurate and precise – as is the estimate for the whole field obtained by combining them. (c) Following on from (b), most sampling effort is directed to the southwest, reducing the confidence interval there, but with little effect on the confidence interval for the southeast. The overall interval is therefore reduced: precision has been improved.

southwest, and that we know that aspect (which way the slope is facing) can affect weed density. Random sampling (or stratified random sampling) ought still to provide an unbiased estimate of density for the field as a whole, but for a given investment in effort, the confidence interval for the estimate will be unnecessarily high. To see why, consider Figure 1.5b. The individual values from samples fall into two groups: high from the southwest slope; low (mostly zero) from the southeast slope. The estimated mean density is close to the true mean (it is accurate), but the variation among samples leads to a very large confidence interval (it is not very precise).

If, however, we acknowledge the difference between the two slopes and treat them separately from the outset, then we obtain means for each that have much smaller confidence intervals. What is more, if we average those means and combine their confidence intervals to obtain an estimate for the field as a whole, then that interval too is much smaller than previously (Figure 1.5b).

But has our effort been directed sensibly, with equal numbers of samples from the southwest slope, where there are lots of weeds, and the southeast slope, where there are virtually none? The answer is no. Remember that narrow confidence intervals arise from a combination of a large number of data points *and* little intrinsic variability (see Box 1.3). Thus, if our efforts had been directed mostly at sampling the southwest slope, the increased amount of data would have noticeably decreased the confidence interval (Figure 1.5c), whereas less sampling of the southeast slope would have made very little difference to that confidence interval because of the low intrinsic variability there. Careful direction of a sampling program can clearly increase overall precision for a given investment in effort. And generally, sampling programs should, where possible, identify biologically distinct subgroups (males and females, old and young, etc.) and treat them separately, but sample at random within subgroups.

## 1.3 Ecology in practice

In previous sections we have established in a general way how ecological understanding can be achieved, and how that understanding can be used to help us predict, manage and control ecological systems. However, the practice of ecology is easier said than done. To discover the real problems faced by ecologists and how they try to solve them, it is best to consider some real research programs in a little detail. While reading the following examples you should focus on how they illuminate our three main points: (i) ecological phenomena occur at a variety of scales; (ii) ecological evidence comes from a variety of different sources; and (iii) ecology relies on truly scientific evidence and the application of statistics. Every other chapter in this book will contain descriptions of similar studies, but in the context of a systematic survey of the driving forces in ecology (Chapters 2–11) or of the application of this knowledge to solve applied problems (Chapters 12–14). For now, we content ourselves with seeking an appreciation of how four research teams have gone about their business.

### 1.3.1 Brown trout in New Zealand: effects on individuals, populations, communities and ecosystems

It is rare for a study to encompass more than one or two of the four levels in the biological hierarchy (individuals, populations, communities, ecosystems). For most of the 20th century, physiological and behavioral ecologists (studying individuals), population dynamicists, and community and ecosystem ecologists tended to follow separate paths, asking different questions in different ways. However, there can be little doubt that, ultimately, our understanding will be enhanced considerably when the links between all these levels are made clear – a point that can be illustrated by examining the impact of the introduction of an exotic fish to streams in New Zealand.

Prized for the challenge they provide to anglers, brown trout (*Salmo trutta*) have been transported from their native Europe all around the world; they were introduced to New Zealand beginning in 1867, and self-sustaining populations are now found in many streams, rivers and lakes there. Until quite recently, few people cared about native New Zealand fish or invertebrates, so little information is available on changes in the ecology of native species after the introduction of trout. However, trout have colonized some streams but not others. We can therefore learn a lot by comparing the current ecology of streams containing trout with those occupied by non-migratory native fish in the genus *Galaxias* (Figure 1.6).

Mayfly nymphs of various species commonly graze microscopic algae growing on the beds of New Zealand streams, but there are some striking differences in their activity rhythms depending on whether they are in *Galaxias* or trout streams. In one experiment, nymphs collected from a trout stream and placed in small artificial laboratory channels were less active during the day than the night, whereas those collected from a *Galaxias* stream were active both day and night (Figure 1.7a). In another experiment, with another mayfly species, records were made of individuals visible in daylight on the surface of cobbles in artificial channels

the individual level –  
consequences for invertebrate  
feeding behaviour



**Figure 1.6**

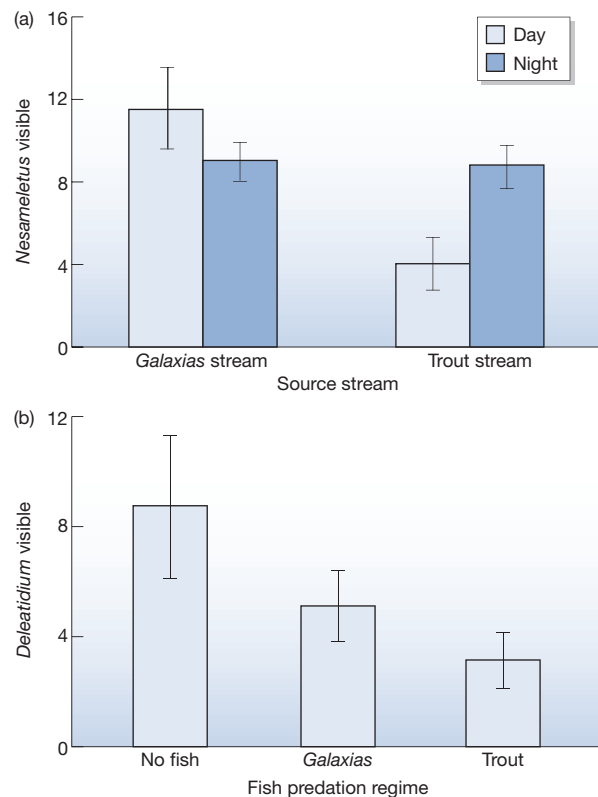
(a) A brown trout and (b) a *Galaxias* fish in a New Zealand stream – is the native *Galaxias* hiding from the introduced predator?

placed in a real stream. Three treatments were each replicated three times – no fish in the channels, trout present and *Galaxias* present. Daytime activity was significantly reduced in the presence of either fish species, but to a greater extent when trout were present (Figure 1.7b).

These differences in activity pattern reflect the fact that trout rely principally on vision to capture prey, whereas *Galaxias* rely on mechanical cues. Thus,

**Figure 1.7**

(a) Mean number ( $\pm$  SE) of *Nesameletus ornatus* mayfly nymphs collected either from a trout stream or a *Galaxias* stream that were recorded by means of video as visible on the substrate surface in laboratory stream channels during the day and night (in the absence of fish). Mayflies from the trout stream are more nocturnal than their counterparts from the *Galaxias* stream. (b) Mean number ( $\pm$  SE) of *Deleatidium* mayfly nymphs observed on the upper surfaces of cobbles during late afternoon in channels (placed in a real stream) containing no fish, trout or *Galaxias*. The presence of a fish discourages mayflies from emerging during the day, but trout have a much stronger effect than *Galaxias*. In all cases, the standard errors were sufficiently small for differences to be statistically significant ( $P < 0.05$ ).



invertebrates in a trout stream are considerably more at risk of predation during daylight hours. And these conclusions are all the more robust because they derive both from the readily controlled conditions of a laboratory experiment and from the more realistic, but more variable, circumstances of a field experiment.

In the Taieri River in New Zealand, 198 sites were selected in a stratified manner by choosing streams of similar dimensions at random in each of three tributaries from each of eight subcatchments of the river. Care was taken not to succumb to the temptation of choosing sites with easy access (near roads or bridges) in case this biased the results. The sites were classified as containing: (i) no fish; (ii) *Galaxias* only; (iii) trout only; or (iv) both *Galaxias* and trout. At every site a variety of physical variables were measured (stream depth, flow velocity, phosphorus concentration in the stream water, percentage of the streambed composed of gravel, etc.). A statistical procedure called multiple discriminant functions analysis was then used to determine which physical variables, if any, distinguished one type of site from another. Means and standard errors of these key environmental variables are presented in Table 1.1.

Trout occurred almost invariably below waterfalls that were large enough to prevent their upstream migration; they tended to occur at low elevations because sites without waterfalls downstream tended to be at lower elevation. Sites containing *Galaxias* (or with no fish) were always upstream of one or several large waterfalls. The few sites that contained both trout and *Galaxias* were below waterfalls, at intermediate elevations, and in sites with cobble beds; the unstable nature of these beds may have promoted coexistence (at low densities) of the two species. This descriptive study at the population level therefore takes advantage of a ‘natural’ experiment (streams that happen to contain trout or *Galaxias*) to determine the effect of the introduction of trout. The most probable reason for the restriction of populations of *Galaxias* to sites upstream of waterfalls, which cannot be climbed by trout, is direct predation by trout on the native fish below the waterfalls (a single small trout in a laboratory aquarium has been recorded consuming 135 *Galaxias* fry in a day).

the population level – brown trout and the distribution of native fish

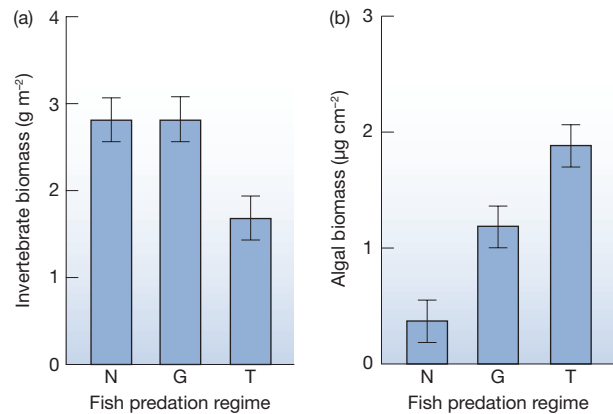
Table 1.1

Means and, in brackets, standard errors for important discriminating variables for fish assemblage classes in 198 sites in the Taieri River. In particular, compare the ‘*Galaxias* only’ and ‘brown trout only’ classes. *Galaxias* are found on their own if there are large waterfalls downstream of the site (and at relatively high elevations where the stream bed has an intermediate representation of cobbles). Brown trout, on the other hand, generally occur where there are no downstream waterfalls (at slightly lower elevations and with a bed composition similar to the *Galaxias* class).

SITE TYPE	NUMBER OF SITES	VARIABLES		
		NUMBER OF WATERFALLS DOWNSTREAM	ELEVATION (m ABOVE SEA LEVEL)	% OF THE BED COMPOSED OF COBBLES
Brown trout only	71	0.42 (0.05)	324 (28)	18.9 (2.1)
<i>Galaxias</i> only	64	12.3 (2.05)	567 (29)	22.1 (2.8)
No fish	54	4.37 (0.64)	339 (31)	15.8 (2.3)
Trout + <i>Galaxias</i>	9	0.0 (0)	481 (53)	46.7 (8.5)

**Figure 1.8**

(a) Total invertebrate biomass and (b) algal biomass (chlorophyll *a*) ( $\pm$  SE) for an experiment performed in summer in a small New Zealand stream. In experimental replicates where trout are present, grazing invertebrates are rarer and graze less; thus, algal biomass is highest. G, *Galaxias* present; N, no fish; T, trout present.



the community – brown trout cause a cascade of effects

That an exotic predator such as trout has direct effects on *Galaxias* distribution or mayfly behavior is not surprising. However, we can ask whether these changes have community consequences that cascade through to other species. In the relatively species-poor stream communities in the south of New Zealand, the plants are mainly algae that grow on the streambed. These are grazed by various insect larvae, which in turn are prey to predatory invertebrates and fish. As we have seen, trout have replaced *Galaxias* in many of these streams. An experiment involving artificial flow-through channels (several meters long, with mesh ends to prevent escape of fish but to allow invertebrates to colonize naturally) placed into a real stream was used to determine whether trout affect the stream food web differently from the displaced *Galaxias*. Three treatments were established (no fish, *Galaxias* present, and trout present, at naturally occurring densities) in each of several randomized blocks located in a stretch of a stream with each block separated by more than 50 m. Algae and invertebrates were allowed to colonize for 12 days before introducing the fish. After a further 12 days, invertebrates and algae were sampled (Figure 1.8).

A significant effect of trout reducing invertebrate biomass was evident ( $P = 0.026$ ), but the presence of *Galaxias* did not depress invertebrate biomass from the no-fish control. Algal biomass, perhaps not surprisingly then, achieved its highest values in the trout treatment ( $P = 0.02$ ). It is clear that trout do have a more pronounced effect than *Galaxias* on invertebrate grazers and, thus, on algal biomass. The indirect effect of trout on algae occurs partly through a reduction in invertebrate density, but also because trout restrict the grazing behavior of the invertebrates that are present (see Figure 1.7b).

the ecosystem – trout and energy flow

The sequence of studies above provided the impetus for a detailed energetics investigation of two neighboring tributaries of the Taieri River (with very similar physicochemical conditions), one being occupied by just trout and the other (because of a waterfall downstream) containing only *Galaxias*. No other fish were present in either stream. The hypothesis under examination was that the rate at which radiation energy was captured through photosynthesis by the algae would be greater in the trout stream because there would be fewer invertebrates and thus a lower rate of consumption of algae. Indeed, annual net ‘primary’ production (the rate of production of plant, in this case algal, biomass) was six times greater in the trout stream than in the *Galaxias* stream (Figure 1.9).



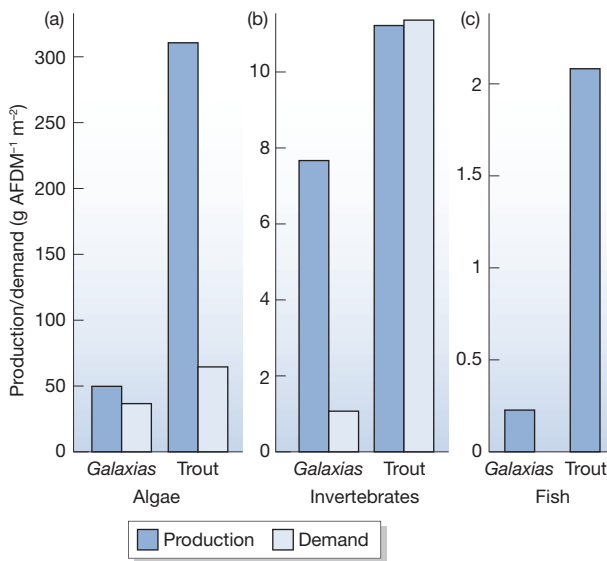


Figure 1.9

Annual estimates for 'production' of biomass at one trophic level, and the 'demand' for that biomass (the amount consumed) at the next trophic level, for (a) primary producers (algae), (b) invertebrates (which consume algae), and (c) fish (which consume invertebrates). Estimates are for a trout stream and a *Galaxias* stream. In the former, production at all trophic levels is higher, but because the trout consume essentially all of the annual invertebrate production (b), the invertebrates consume only 21% of primary production (a). In the *Galaxias* stream, these fish consume only 18% of invertebrate production, 'allowing' the invertebrates to consume the majority (75%) of annual primary production.

Moreover, the primary consumers (invertebrates that eat algae) produced new biomass in the trout stream at about 1.5 times the rate in the *Galaxias* stream, while trout themselves produced new biomass at roughly nine times the rate that *Galaxias* do (Figure 1.9).

Thus, the algae, invertebrates and fish are all 'more productive' in the trout stream than in the *Galaxias* stream; but *Galaxias* consume only about 18% of available prey production each year (compared to virtually 100% consumption by trout); while the grazing invertebrates consume about 75% of primary production in the *Galaxias* stream (compared to only about 21% in the trout stream) (Figure 1.9). Thus, the initial hypothesis appears to be confirmed: it is strong control by trout of the invertebrates that releases algae to produce and accumulate biomass at a fast rate.

A further ecosystem consequence ensues: in the trout stream, the higher primary production is associated with a faster rate of uptake by algae of plant nutrients (nitrate, ammonium, phosphate) from the flowing stream water (Simon et al., 2004).

This series of studies, therefore, illustrates some of the variety of ways in which ecological investigations may be pursued, and both the range of levels in the biological hierarchy that ecology spans and the way in which studies at different levels may complement one another. While it is necessary to be cautious when interpreting the results of an unreplicated study (only one trout and one *Galaxias* stream in the 'ecosystem study'), the conclusion that a trophic cascade is responsible for the patterns observed at the ecosystem level can be made with some confidence because of the variety of other corroborative studies conducted at the individual, population and community levels. Although brown trout are exotic invaders in New Zealand, and they have far-reaching effects on the ecology of native ecosystems, they are now considered a valuable part of the fauna, particularly by anglers, and generate millions of dollars for the nation. Many other invaders have dramatic negative economic impacts (Box 1.5).





## 1.5 TOPICAL ECONCERNS

### 1.5 Topical ECONcerns

#### Invasions and homogenization of the biota: does it matter?

A recent analysis concluded that tens of thousands of invading exotic species in the United States cause economic losses totaling \$137 billion each year (Pimentel et al., 2000). Table 1.2 breaks down the total into a variety of taxonomic groups.

Let us consider a few invaders with particularly dramatic consequences. The yellow star thistle (*Centaurea solstitialis*) now dominates more than 4 million hectares in California, resulting in the total loss of once productive grassland. Rats are estimated to destroy \$19 billion of stored grains nationwide per year, as well as causing fires (by gnawing electric wires), polluting foodstuffs, spreading diseases and preying on native species. Introduced carp reduce water quality by increasing turbidity, while 44 native fish are threatened or endangered by fish invaders. The red fire ant (*Solenopsis invicta*) kills poultry, lizards, snakes and ground-nesting birds; in Texas alone, its estimated damage to livestock, wildlife and public health is put at about \$300 million per year, and a further \$200 million is spent on control. The zebra mussel (*Dreissena polymorpha*), which arrived in Michigan's Lake St. Clair in ballast water released from ships from Europe, has reached most aquatic

habitats in the eastern United States, and is expected to spread nationwide in the next 20 years. The large populations that develop threaten native mussels and other fauna, not only by reducing food and oxygen availability but by physically smothering them. The mussels also invade and clog water intake pipes, so that millions of dollars need to be spent clearing them from water filtration and hydroelectric generating plants. Overall, pests of crop plants, including weeds, insects and pathogens, engender the biggest economic costs. However, imported human disease organisms, particularly HIV and influenza viruses, cost \$6.5 billion to treat and result in 40,000 deaths per year. (See Pimentel et al., 2000, for further details and references.)

*Globalization has been the prevalent economic ideology in recent times. Globalization of the biota, in which successful invaders are moved around the world, often driving local species extinct, can be expected to lead to a general homogenization of the world's biota. [Lövei (1997) has colorfully referred to this as 'McDonaldization' of the biosphere.] Does biotic homogenization matter? Why?*

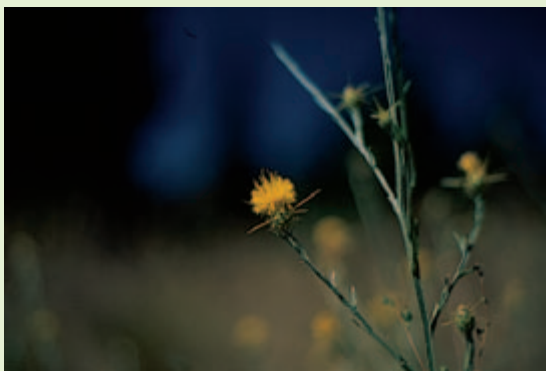
**Table 1.2**

Estimated annual costs (billions of dollars) associated with invaders in the United States.

TYPE OF ORGANISM	NUMBER OF INVADERS	MAJOR CULPRITS	LOSS AND DAMAGE	CONTROL COSTS	TOTAL COSTS
Plants	5,000	Crop weeds	24.4	9.7	34.1
Mammals	20	Rats and cats	37.2	NA	37.2
Birds	97	Pigeons	1.9	NA	1.9
Reptiles and amphibians	53	Brown tree snake	0.001	0.005	10.006
Fishes	138	Grass carp, etc.	1.0	NA	1.0
Arthropods	4,500	Crop pests	17.6	2.4	20.0
Mollusks	88	Asian clams	1.2	0.1	1.3
Microbes (pathogens)	>20,000	Crop pathogens	32.1	9.1	41.2

NA, not available.  
AFTER PIMENTEL ET AL., 2000

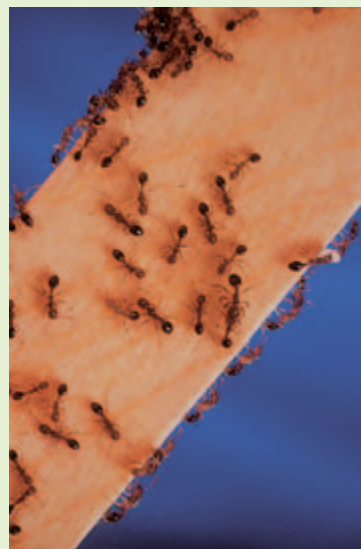
© GREG HODSON, VISUALS UNLIMITED 126948

Yellow star thistle, *Centaurea solstitialis*.

© VISUALS UNLIMITED/INR 127038

Zebra mussels, *Dreissena polymorpha*.

© VISUALS UNLIMITED/ARS 127002

Red fire ants, *Solenopsis*.

### 1.3.2 Successions on old fields in Minnesota: a study in time and space

‘Ecological succession’ is a concept that must be familiar to many who have simply taken a walk in open country – the idea that a newly created habitat, or one in which a disturbance has created an opening, will be inhabited, in turn, by a variety of species appearing and disappearing in some recognizably repeatable sequence. Widespread familiarity with the idea, however, does not mean that we understand fully the processes that drive or fine-tune successions; yet developing such understanding is important not just because succession is one of the fundamental forces structuring ecological communities, but also because human disturbance of natural communities has become ever more frequent and profound. We need to know how communities may respond to, and hopefully recover from, such disturbance, and how we may aid that recovery.

One particular focus for the study of succession has been the old agricultural fields of the eastern USA, abandoned as farmers moved west in search of ‘fresh fields and pastures new’. One such site is now the Cedar Creek Natural History Area, roughly 50 km north of Minneapolis, Minnesota. The area was first settled by Europeans in

the use of natural  
experiments . . .

1856 and was initially subject to logging. Clearing for cultivation then began about 1885, and land was first cultivated between 1900 and 1910. Now there are agricultural fields that are still under cultivation and others that have been abandoned at various times since the mid-1920s. Cultivation led to depletion of nitrogen from soils that already were naturally poor in this important plant nutrient.

In the first place, studies at Cedar Creek illustrate the value of ‘natural experiments’. To understand the successional sequence of plants that occur in fields in the years following abandonment we *could* plan an artificial manipulation, under our control, in which a number of fields currently under cultivation were ‘forcibly’ abandoned and the communities in them sampled repeatedly into the future. (We would need a number of fields because any single field might be atypical, whereas several would allow us to calculate mean values for, say, ‘number of new species per year’, and place confidence intervals around those means.) But the results of this experiment would take decades to accumulate. The natural experiment alternative, therefore, was to use the fact that records already exist of when many of the old fields were abandoned. This is what Tilman and his team did. Thus, Figure 1.10 illustrates data from a group of 22 old fields surveyed in 1983, having been abandoned at various times between 1927 and 1982 (i.e. between 1 and 56 years previously). Interpreted cautiously, these can be treated as 22 ‘snapshots’ of the continuous process of succession in old fields at Cedar Creek in general, even though each field was itself only surveyed once.

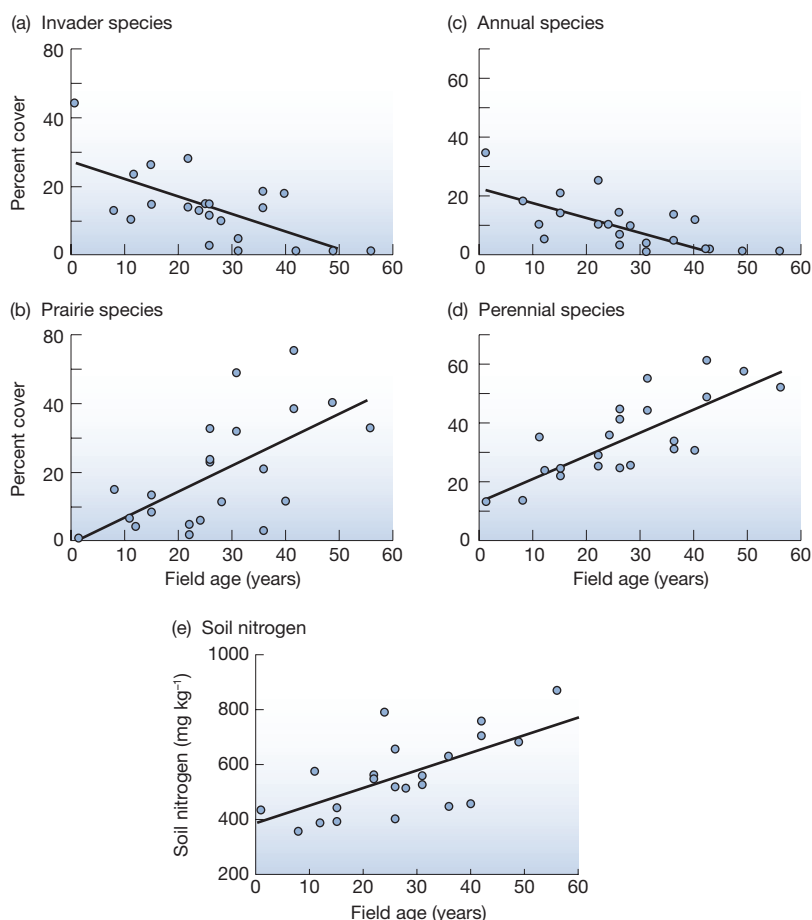
A number of the shifting balances during succession are clear from the figure as statistically significant trends. Over the 56 years, the cover of ‘invader’ species (mostly agricultural weeds) decreased (Figure 1.10a) while the cover of species from nearby prairies increased (Figure 1.10b): the natives reclaimed their land. Of more general applicability, the cover of annual species decreased over time, while the cover of perennial species increased (Figure 1.10c, d). Annual species (those that complete a whole generation from seed to adult through to seeds again within a year) tend to be good at increasing in abundance rapidly in relatively empty habitats (the early stages of succession); whereas perennials (those that live for several or many years and may not reproduce in their early years) are slower to establish but more persistent once they do.

. . . in generating correlations

On the other hand, natural experiments like this, while frequently suggestive and stimulating (and too good an opportunity to miss), usually only generate *correlations*. They may therefore fail to establish what actually causes the observed patterns. In the present case, we can see the problem by noting, first, that field age is itself strongly correlated with nitrogen concentration in the soil – perhaps the single most important plant nutrient (Figure 1.10e). The question therefore arises: are the correlations in Figure 1.10a–d the result of an effect of field age itself? Or is the causal agent nitrogen, with which age is correlated?

artificial experiments:  
the search for causation

Manipulative field experiments can be used to help support – or refute – what so far is no more than a plausible explanation based on correlation. It seems to follow from the proposed explanation (time matters) that nitrogen itself has little role to play in driving these successions, and that manipulating nitrogen should do little to alter the species sequences that these fields have followed. To test this, Tilman’s team selected a pair of fields (one abandoned for 46 years and the other for 14 years) and, over a 10-year period starting in 1982, subjected six replicate 4 m × 4 m plots in each field to one of two treatments: nitrogen added at rates of either 1 or 17 g m<sup>-2</sup> yr<sup>-1</sup> (Inouye & Tilman, 1995). Two questions in particular were being asked.

**Figure 1.10**

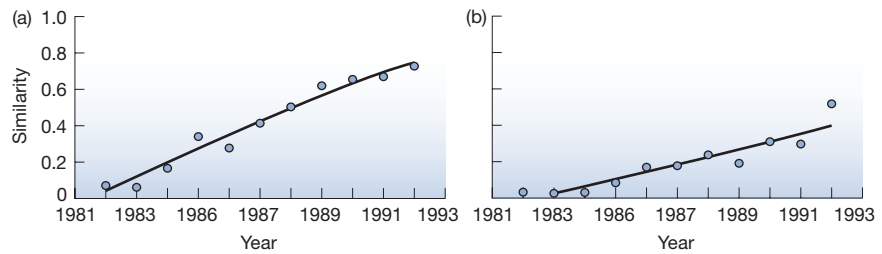
Twenty-two fields at different stages in an old-field succession were surveyed to generate the following trends with successional stage (field age): (a) invader species decreased, (b) native prairie species increased, (c) annual species decreased, (d) perennial species increased, and (e) soil nitrogen content increased. The best fit lines (see Box 1.2) are highly significant in every case ( $P < 0.01$ ).

- 1 Do patches receiving different supply rates of nitrogen become less similar in species composition over time?
- 2 Do patches receiving similar supply rates of nitrogen become more similar in species composition over time?

The answer to the first question was clear: plots within a field were initially similar to one another but, 10 years later, plots receiving different amounts of nitrogen had diverged in species composition – and the greater the difference in nitrogen input, the greater the divergence (Inouye & Tilman, 1995).

The answer to the second question is illustrated in Figure 1.11. At the start of the experiment, the field abandoned for 46 was very different in species composition to the one only abandoned for 14 years. But 10 years later, plots within the two fields that had been subjected to similar rates of nitrogen input had become remarkably similar (Figure 1.11).

Thus, this experiment tends to refute the simplicity of our proposed explanation. Time itself is not the only cause of successional changes in species composition of these old fields. Differences in available nitrogen cause successions to diverge; similarities cause them to converge much more quickly than they would otherwise do. Time (= opportunity to colonize) and nitrogen are clearly intimately



**Figure 1.11**

Results from an experiment in which plots within two old fields from Figure 1.10 were given artificial nitrogen addition treatments starting in 1982: one of the fields had been abandoned for 46 years and the other for 14 years. (a) Between 1982 and 1992, plots receiving  $17 \text{ g of nitrogen m}^{-2} \text{ yr}^{-1}$  in the two fields became increasingly similar in composition. The similarity index measures the extent to which the species composition in the pair of fields is similar – identical compositions produce a similarity index of 1, entirely different compositions produce a similarity of 0. (b) Like (a) but with only  $1 \text{ g of nitrogen m}^{-2} \text{ yr}^{-1}$ . Note in this case that there was still convergence in species composition between the two fields but to a lesser extent. In both cases the best fit lines are highly significant.

AFTER INOUE & TILMAN, 1995

insight into the effects of  
nitrogen pollution

intertwined and further experiments will be required to disentangle their web of cause and effect – just one of many unanswered ecological questions.

Finally, experimental manipulations over extended periods like these may also provide important insights into the possible effects of more chronic human disturbances to natural communities. The lower rate of nitrogen addition in the experiment ( $1 \text{ g of nitrogen m}^{-2} \text{ yr}^{-1}$ ) was similar to that experienced in many parts of the world as a result of increased atmospheric deposition of inorganic nitrogen (mainly derived from the burning of fossil fuels). Even these low levels apparently led to convergence of previously dissimilar communities over a 10-year period (Figure 1.11b). Experiments like this are crucial in helping us to predict the effects of pollutants, a point that is taken further in the next example.

### 1.3.3 Hubbard Brook: a long-term commitment of large-scale significance

The Cedar Creek study took advantage of a temporal pattern (a succession that takes decades to run its course) being reflected more or less accurately by a pattern in space (fields abandoned for different periods). The spatial pattern has the advantage that it could be studied within the time-bite of most research projects (3–5 years). It would have been better still to follow the ecological pattern through time but rather few researchers or institutions have risen to the challenge of designing research programs that last for decades.

A notable exception has been the work of Likens and associates at the Hubbard Brook Experimental Forest, an area of temperate deciduous forest drained by small streams in the White Mountains of New Hampshire in the USA. The researchers were pioneers with no precedents to follow. They decided to think big, and their work has shown the value of large-scale studies and long-term data records. The study commenced in 1963 and continues to the present. In the second edition of their classic book *Biogeochemistry of a Forested Ecosystem*, Likens and Bormann (1995) make poignant reference to three of their original collaborators who had died since the study began. Long term indeed.



**Figure 1.12**

The Hubbard Brook experimental forest. Note the experimental stream catchment from which all trees were removed – extending from the top left toward the center of the photograph.

The research team developed an approach called ‘the small watershed technique’ to measure the input and output of chemicals from individual catchment areas in the landscape. Because many chemical losses from terrestrial communities are channeled through streams, a comparison of the chemistry of stream water with that of incoming precipitation can reveal a lot about the differential uptake and cycling of chemical elements by the terrestrial biota. The same study can reveal much about the sources and concentrations of chemicals in the stream water, which in turn may influence the productivity of stream algae and the distribution and abundance of stream animals.

The catchment area (or watershed) – the extent of terrestrial environment drained by a particular stream – was taken as the unit of study because of the role that streams play in chemical export from the land. Six small catchments were defined and their outflows were monitored (Figure 1.12). A network of precipitation gauges recorded the incoming amounts of rain, sleet and snow. Chemical analyses of precipitation and stream water made it possible to calculate the amounts of various chemical elements entering and leaving the system. In most cases, the output of chemicals in streamflow was greater than their input from rain, sleet and snow (Table 1.3). The source of the excess chemicals was weathering of parent rock and soil, estimated at about  $70 \text{ g m}^{-2} \text{ yr}^{-1}$ . The exception was nitrogen; less was exported in stream water than was added to the catchment in precipitation and by fixation of atmospheric nitrogen by microorganisms in the soil.

Likens had the brilliant idea of performing a large-scale experiment in which all the trees were felled in one of Hubbard Brook’s six catchments. In terms of experimental design, statistical purists might argue the study was flawed because

the catchment area as a unit of study

insights from a large-scale field experiment

**Table 1.3**

Annual chemical budgets for forested catchment areas at Hubbard Brook ( $\text{kg ha}^{-1} \text{ yr}^{-1}$ ). Inputs are for dissolved materials in precipitation or in dryfall (gases or associated with particles falling from the atmosphere). Outputs are losses in stream water as dissolved material plus particulate organic material in the streamflow. The source of the excess chemicals (where outputs exceeded inputs) was weathering of parent rock and soil. The exception was nitrogen (as ammonium or nitrate ions) – less was exported than arrived in precipitation because of nitrogen uptake in the forest.

	$\text{NH}_4^+$	$\text{NO}_3^-$	$\text{SO}_4^{2-}$	$\text{K}^+$	$\text{Ca}^{2+}$	$\text{Mg}^{2+}$	$\text{Na}^+$
Input	2.7	16.3	38.3	1.1	2.6	0.7	1.5
Output	0.4	8.7	48.6	1.7	11.8	2.9	6.9
Net change*	+2.3	+7.6	-10.3	-0.6	-9.2	-2.2	-5.4

\*Net change is positive when the catchment gains matter and negative when it loses it.

AFTER LIKENS ET AL., 1971

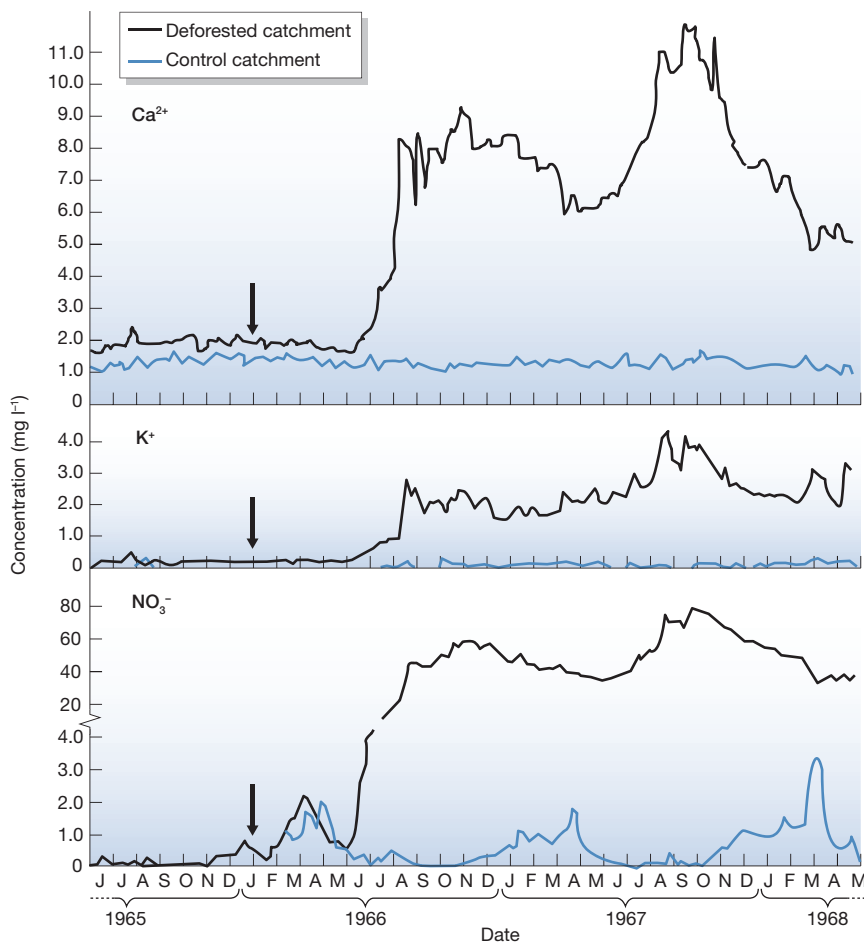
it was unreplicated. However, the scale of the undertaking rather precluded replication. In any case, it was the asking of a dramatically new question that made this study a classic rather than elegant statistical design.

Within a few months of felling all the trees in the drainage basin, the consequences were evident in the stream water. The overall export of dissolved inorganic substances from the disturbed catchment rose to 13 times the normal rate (Figure 1.13). Two phenomena were responsible. First, the enormous reduction in transpiring surfaces (leaves) led to 40% more precipitation passing through the ground water to be discharged to the streams, and this increased outflow caused greater rates of leaching of chemicals and weathering of rock and soil. Second, and more significantly, deforestation effectively broke the link between decomposition and nutrient uptake. In the spring, when the deciduous trees would normally have started production and taken up inorganic nutrients released by decomposer activity, these were instead available to be leached in the drainage water.

Likens knew from the beginning that the rain and snow at Hubbard Brook were quite acid but it was some years before the widespread nature of acid rain in North America became clear. In fact, Hubbard Brook is more than 100 km from the nearest urban industrial area, yet precipitation and stream water were both markedly acid as a result of atmospheric pollution from fossil fuels. The long-term records kept so meticulously since 1963 at Hubbard Brook have proved invaluable in monitoring progress in the war against acid rain and its long-term consequences. The value of such records of stream water concentrations can be seen for hydrogen, sulfate and nitrate, three ions associated with acid rain (which in simple terms is a mixture of dilute nitric and sulphuric acids; sulphuric acid is the dominant acid in the eastern USA). There have been statistically significant declines in average annual concentrations of  $\text{H}^+$  and  $\text{SO}_4^{2-}$  since 1964/65, and also of  $\text{NO}_3^-$ , though the latter is subject to much greater year to year variation (Figure 1.14). Of note, however, is the fact that the results for shorter periods suggest quite different trends. Consider the hydrogen ion graph where three periods of 4 years are highlighted in different colors. The first suggests an increasing trend, the second no change and the third a decreasing trend. In fact, no statistically significant, long-term trend was established until nearly two decades of data had been amassed (Likens, 1989).

for statistically significant trends to become evident, many years of data may be required



**Figure 1.13**

Concentrations of ions in stream water from the experimentally deforested watershed 2 and the control (unmanipulated) watershed 6 at Hubbard Brook. The timing of deforestation is indicated by arrows. In each case, there was a dramatic increase in export of the ions after deforestation. Note that the 'nitrate' axis has a break in it.

AFTER LIKENS & BORMANN, 1975

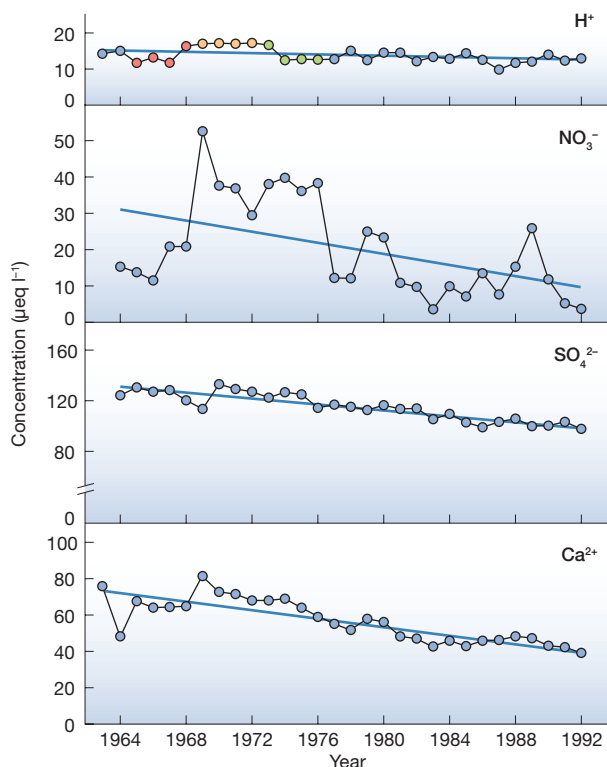
It is thought that acid rain began in the USA in the early 1950s (before monitoring began at Hubbard Brook). After the passage of the Clean Air Act in 1970, emissions of SO<sub>2</sub> and particulates were reduced and this has been clearly reflected in stream water chemistry (Figure 1.14). Additional reductions in emissions have occurred as a result of the 1990 amendments to the Clean Air Act. However, critical questions remain – will forest and aquatic ecosystems recover from the effects of acid rain, and if so how long will it take (Likens et al., 1996)?

Using long-term data from Hubbard Brook and predictions of reductions to SO<sub>2</sub> emissions as a result of government legislation, Likens and Bormann (1995) estimated that by the turn of the millennium the sulfur loading in the atmosphere would still be three times higher than values recommended for protection of sensitive forests and aquatic communities (many plants, fish and aquatic invertebrates are intolerant of acid conditions). Moreover, declining inputs to Hubbard Brook of basic cations, such as calcium, may be causing the forests and streams to become even more sensitive to acidic inputs. Likens and Bormann (1995) hypothesized that a dramatic decline in forest growth rates during recent years may be related to a decline in calcium in the soil, a critical nutrient for tree growth. Acid rain may be responsible for the calcium deficiency.

long data runs reveal the history of acid rain

**Figure 1.14**

Long-term changes in concentrations [microequivalents ( $\mu\text{eq}$ )  $\text{l}^{-1}$ ] of  $\text{H}^+$ ,  $\text{NO}_3^-$ ,  $\text{SO}_4^{2-}$  and  $\text{Ca}^{2+}$  in stream water from Hubbard Brook watershed 6 from 1963/64 to 1992/93. The declines are related to reductions in 'acid rain' affecting the Hubbard Brook area. The regression lines for all these ions have a probability of being significantly different from zero (no change) of  $P < 0.05$ ; in other words there is a statistically significant pattern of decline in each. However, many years of data were needed before these patterns could be convincingly demonstrated. This is particularly marked for the hydrogen ion graph, where three periods of 4 years are highlighted in different colors. The first (in red) suggests an increasing trend, the second (in orange) no change and the third (in green) a decreasing trend.



AFTER LIKENS &amp; BORMANN, 1995

An associated reduction in bird populations in the forest may even be linked to this scenario. These unanswered questions are the subject of new phases of research at Hubbard Brook.

### 1.3.4 A modeling study: to discover why Asian vultures were heading for extinction

In 1997, vultures in India and Pakistan began dropping from their perches. Local people were quick to notice dramatic declines in numbers of the oriental white-backed vulture *Gyps bengalensis* (Figure 1.15) and the long-billed vulture *G. indicus*, but ecologists were puzzled. Repeated population surveys from 2000 to 2003 confirmed alarming rates of decline, defined technically as values of the 'population growth rate',  $\lambda$  (where the population size  $N$  in year  $t$  equals  $\lambda$  times the population size the previous year,  $t - 1$ ; in other words  $\lambda = N_t/N_{t-1}$ ). For the oriental white-backed vulture in India  $\lambda$  was 0.52 and in Pakistan it was 0.50, equating to a 48% and 50% decline per year, respectively. The state of affairs was a little less disastrous for the long-billed vulture in India where  $\lambda$  was 0.78, equating to a 22% decline per year.

vulture populations in India and Pakistan were declining by 22–50% per year

These population crashes were of very great concern because of the crucial role vultures play in everyday life, disposing of the dead bodies of large animals, both wild and domestic. The loss of vultures enhanced carrion availability to wild dogs and rats, allowing their populations to increase and raising the probability of diseases such as rabies and plague being transmitted to humans. Moreover,

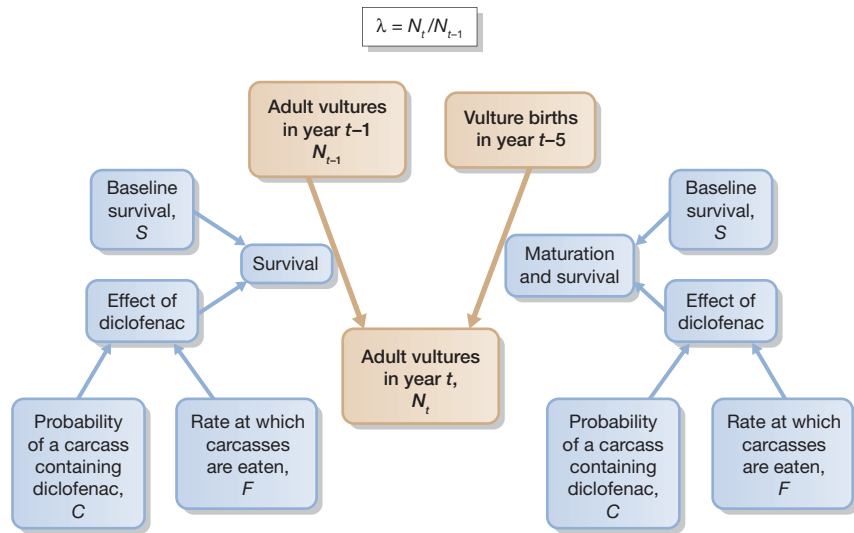
contamination of nearby wells and the spread of disease by flies became more likely now that dead animals were not quickly picked clean by vultures. One group of people, the Parsees, were even more intimately affected because their religion calls for the dead to be taken in daylight to a special tower (dakhma) where the body is stripped clean by vultures within a few hours. It was crucial for ecologists to quickly determine the cause of vulture declines so that action could be taken.

It took a few years to find a common element in the deaths of otherwise healthy birds – each had suffered from visceral gout (accumulation of uric acid in the body cavity) followed by kidney failure. Soon a crucial piece in the jigsaw became clear: vultures dying of visceral gout contained residues of the drug diclofenac (Oaks et al., 2004). Then it was confirmed that carcasses of domestic animals treated with diclofenac were lethal to captive vultures. Diclofenac, a non-steroidal anti-inflammatory drug developed for human use in the 1970s, had only recently come into common use as a veterinary medicine in Pakistan and India. Thus, a drug that benefited domestic mammals proved lethal to the vultures that fed on their bodies.

The circumstantial evidence was strong, but given the relatively small numbers of diclofenac-contaminated dead bodies available to wild vultures, was the associated vulture mortality sufficient explanation for the population crashes? Or might other factors also be at play? This was the question addressed by Green and his team (2004) by means of a simulation population model. On the basis of their surveys of population declines and knowledge of birth, death and feeding rates, the researchers built a model to predict the behavior of the vulture populations. We show their model as a flow diagram (Figure 1.15); Green and his team developed mathematical formulae to predict changes in population size, but the details need not concern us here. The researchers posed the specific question: what proportion of carcasses ( $C$ ) would have to contain lethal doses of diclofenac to cause the observed population declines? Their simulation model included the following assumptions:

... caused by drug-contaminated carcasses?

- 1 *Gyps* vultures do not breed (i.e. become adult) until they are 5 years old and then are capable of rearing only one juvenile per year, but only if both parents survive the breeding season of 160 days.
- 2 The fate of the population depends not only on rates of birth but also death. The pre-diclofenac ‘baseline’ survival rate of adult vultures ( $S$ ) fell in the range 0.90–0.97, typical for large-bodied, long-lived birds. In other words, in the absence of diclofenac deaths, only 3–10% of adult vultures die each year.
- 3 Diclofenac poisoning reduces survival rate further. This depends on the probability an adult will eat from a diclofenac-affected carcass. In turn, this depends partly on the proportion of carcasses in the environment that contain diclofenac ( $C$ ) and partly on how often vultures feed ( $F$ , the interval in days between feeding). Note that a single meal can sustain a vulture for 3 days and they do not feed every day;  $F$  ranges from 2 to 4 days. Vultures that feed more often (more times per year) are more likely to feed from a diclofenac-affected carcass and die.
- 4 The researchers had real estimates for population sizes in different years ( $N$ ) and hence of  $\lambda$  (see above). In their modeling exercise they systematically varied the values for baseline survival  $S$  and feeding rate  $F$ . This is because



**Figure 1.15**

Flow diagram showing the elements of a model of how the number of adult vultures in the population changes from one year ( $N_{t-1}$ ) to the next ( $N_t$ ). The oriental white-backed vulture, whose populations have shown disastrous declines in India and Pakistan, is shown in the inset. The number of adult vultures in year  $t$  depends on the number present the previous year ( $t-1$ ), some of which die from natural causes (baseline survival) and others because of diclofenac poisoning. The number of adults in year  $t$  also depends on the number of vultures born 5 years previously ( $t-5$ ), because vultures do not mature until they are 5 years old. Again, some newborn vultures die before maturity from natural causes and others because of diclofenac poisoning. The reduction in survival due to diclofenac depends on two things: the probability that a carcass contains diclofenac ( $C$ ) and the rate at which carcasses are eaten ( $F$ ).

they did not know precisely what the baseline survival or feeding rates were in these particular populations, although they did know the range in which the values fell. Thus, they ran the model for values of baseline survival of 0.90, 0.95 and 0.97, and with intervals between feeding of 2, 3 and 4 days.

- 5 Once all these parameters were entered into their model, the researchers could calculate the ‘missing’ parameter  $C$  – the proportion of carcasses that needs to be contaminated with diclofenac to account for the observed rate of population decline,  $\lambda$  (Table 1.4).

simulation models show that diclofenac-contaminated cattle are sufficient to explain vulture losses

Table 1.4 shows that at a maximum (for the Pakistani oriental white-backed vultures when adult survival is set at 0.97 and feeding interval is 4 days) only 0.743% or, in other words, 1 in 135 carcasses have to be dosed with diclofenac to cause the observed population decline. At a minimum (for Indian long-billed vultures when adult survival is set at 0.90 and feeding interval is 2 days) only 0.132% or 1 in 757 contaminated carcasses are required. The proportions of vultures found dead or dying in the wild with signs of diclofenac poisoning were closely similar to the proportions of deaths expected from the model if the observed population decline was due *entirely* to diclofenac poisoning. The researchers concluded, therefore, that diclofenac poisoning was a sufficient cause for the dramatic decline of wild vultures.

Clearly, urgent action is needed to prevent the exposure of vultures to live-stock carcasses contaminated with diclofenac and the Punjab government, for

**Table 1.4**

Modeled percentages of animal carcasses with lethal levels of diclofenac required to cause population declines at rates,  $\lambda$ , observed for long-billed vultures (LBV) or oriental white-backed vultures (OWBV) in India and Pakistan between 2000 and 2003. A value of 0.132%, for example, means that only 1 in 757 carcasses needs to be contaminated to cause the vulture decline. For each population, results are given for three feasible baseline adult survival rates,  $S$  (i.e. in the absence of diclofenac) and three values of the interval between vulture feeding bouts in days,  $F$ .

	$F$	PERCENTAGE OF CARCASSES WITH LETHAL LEVEL		
		$S = 0.90$	$S = 0.95$	$S = 0.97$
LBV India	2	0.132	0.135	0.137
	3	0.198	0.202	0.205
	4	0.263	0.271	0.273
OWBV India	2	0.339	0.347	0.349
	3	0.508	0.521	0.526
	4	0.677	0.693	0.699
OWBV Pakistan	2	0.360	0.368	0.372
	3	0.538	0.551	0.558
	4	0.730	0.734	0.743

example, has now banned its use. Green and his colleagues also highlighted the need for research to identify alternative drugs that are effective in livestock and safe for vultures. Swan et al. (2006) have since tested a drug called meloxicam with promising results. Finally, given the depths to which the vulture populations have sunk, Green's team emphasize the importance of breeding vultures in captivity until diclofenac is under control. This is a sensible precaution to ensure long-term survival and to provide for future reintroduction programs.

This example, then, has illustrated a number of important general points about mathematical models in ecology:

- 1 Models can be valuable for exploring scenarios and situations for which we do not have, and perhaps cannot expect to obtain, real data (e.g. what would be the consequences of different baseline survival or feeding rates?).
- 2 They can be valuable, too, for summarizing our current state of knowledge and generating predictions in which the connection between current knowledge, assumptions and predictions is explicit and clear (given various values for  $S$  and  $F$ , and knowing  $\lambda$ , what values of  $C$  do these imply?).
- 3 In order to be valuable in these ways, a model does not have to be (indeed, cannot possibly be) a full and perfect description of the real world it seeks to mimic – all models incorporate approximations (the vulture model was, of course, a very 'stripped down' version of its true life history).
- 4 Caution is therefore always necessary – all conclusions and predictions are provisional and can be no better than the knowledge and assumptions on which they are based – but applied cautiously they can be useful (the vulture model prompted changes in management practices and research into new drugs).
- 5 Nonetheless, a model is inevitably applied with much more confidence once it has received support from real sets of data.



## Summary

# SUMMARY

### Ecology as a pure and applied science

We define ecology as the scientific study of the distribution and abundance of organisms and the interactions that determine distribution and abundance. From its origins in prehistory as an 'applied science' of food gathering and enemy avoidance, the twin threads of pure and applied ecology have developed side by side, each depending on the other. This book is about how ecological understanding is achieved, what we do and do not understand, and how that understanding can help us predict, manage and control.

### Questions of scale

Ecology deals with four levels of ecological organization: individual organisms, populations (individuals of the same species), communities (a greater or lesser number of populations) and ecosystems (the community together with its physical environment). Ecology can be done at a variety of spatial scales, from the 'community' within an individual cell to that of the whole biosphere. Ecologists also work on a variety of time scales. Ecological succession, for example, may be studied during the decomposition of animal dung (weeks), or during the period of climate change since the last ice age (millennia). The normal period of a research program (3–5 years) may often miss important patterns that occur over long time scales.

### Diversity of ecological evidence

Many ecological studies involve careful observation and monitoring, in the natural environment, of the changing abundance of one or more species over time, or through space, or both. Establishing the cause(s) of patterns observed often requires manipulative field experiments. For complex ecological systems (and most of them are) it will often be appropriate to construct simple laboratory systems that can act as jumping-off points in our search for understanding. Mathematical models of ecological communities also have an important role to play in unraveling ecological complexity. However, the worth of models and simple laboratory experiments must always be judged in terms of the light they throw on the working of natural systems.

### Statistics and scientific rigor

What makes the science of ecology rigorous is that it is based not on statements that are simply assertions, but on conclusions that are the results of carefully planned investigations with well thought-out sampling regimes, and on conclusions, moreover, to which a level of statistical confidence can be attached. The term that is most often used, at the end of a statistical test, to measure the strength of conclusions being drawn is a '*P*-value' or probability level. The statements ' $P < 0.05$ ' (significant) or ' $P < 0.01$ ' (highly significant) mean that these are studies where sufficient data have been collected to establish a conclusion in which we can be confident.

### Ecology in practice

Studies of the impacts of brown trout, introduced to New Zealand in the 20th century, have spanned all four ecological levels (individuals, populations, communities, ecosystems). Trout have replaced populations of native galaxiid fish below waterfalls. Laboratory and field experiments have established that grazing invertebrates in trout streams show an individual response, spending more time hiding and less time grazing. Trout cause a cascading community effect because the grazers impact less on the algae. Finally, a descriptive study revealed an ecosystem consequence: primary productivity by algae is higher in a trout stream than a galaxiid stream.

In the Cedar Creek Natural History Area are agricultural fields that are still under cultivation and others that have been abandoned at various times since the mid-1920s. This natural experiment was exploited to provide a description of the species sequence associated with succession on such abandoned fields. However, the fields differed not only in age but also in soil nitrogen. A set of field experiments, where soil nitrogen was augmented in a systematic way in fields of different age, showed that time and nitrogen interacted to cause the observed successional sequences.

The Hubbard Brook Experimental Forest study has been running since 1963. A large-scale experiment,



involving the felling of all the trees in a single catchment area, resulted in a dramatic increase in chemical concentrations (particularly nitrate) in stream water. The loss of nitrate from the land and its increase in water can be expected to have consequences for the communities on both sides of the land–water interface. Monitoring of chemical concentrations for more than four decades in undisturbed catchments has revealed how acid rain has been diminishing as a result of the Clean Air Act. However, neither the forest nor the streams are immune from continuing effects of the pollution that caused acid rain.

Disturbing declines in vulture populations have profound implications for public health in India and

Pakistan. A common element in the deaths was visceral gout, traced to an adverse effect of diclofenac used by veterinarians to treat domestic cattle, one source of food for vultures. Given the relatively small numbers of diclofenac-contaminated dead bodies available to wild vultures, a mathematical model was run to determine whether deaths due to diclofenac were a sufficient explanation for the population crashes, or whether other factors might also be at play. In fact, the proportion of vultures dying from diclofenac poisoning was very similar to that expected from the model if the decline was due *entirely* to diclofenac poisoning. Steps have now been taken to remedy the situation.

## Review questions

### REVIEW QUESTIONS

Asterisks indicate challenge questions

- 1\* Discuss the different ways that ecological evidence can be gained. How would you go about trying to answer one of ecology's unanswered questions, namely 'Why are there more species in the tropics than at the poles'?
- 2\* The variety of microorganisms that live on your teeth have an ecology like any other community. What do you think might be the similarities in the forces determining species richness (the number of species present) in your oral community as opposed to a community of seaweeds living on boulders along the shoreline?
- 3 Why do some temporal patterns in ecology need long runs of data to detect them, while other patterns need only short runs of data?
- 4 Discuss the pros and cons of descriptive studies as opposed to laboratory studies of the same ecological phenomenon.
- 5 What is a 'natural field experiment'? Why are ecologists keen to take advantage of them?
- 6 Search the library for a variety of definitions of ecology: which do you think is most appropriate and why?
- 7\* In a study of stream ecology, you need to choose 20 sites to test the hypothesis that brown trout have higher densities where the streambed consists of cobbles. How might your results be biased if you chose all your sites to be easy to access because they are near roads or bridges?
- 8 How might the results of the Cedar Creek study of old-field succession have been different if a single field had been monitored for 50 years, rather than simultaneously comparing fields abandoned at different times in the past?
- 9\* When all the trees were felled in a Hubbard Brook catchment, there were dramatic differences in the chemistry of the stream water draining the catchment. How do you think stream chemistry would change in subsequent years as plants begin to grow again in the catchment area?
- 10 What are the main factors affecting the confidence we can have in predictions of a mathematical model?



# Chapter 2



## Ecology's evolutionary backdrop

### *Chapter contents*

#### CHAPTER CONTENTS

- 2.1 Introduction
- 2.2 Evolution by natural selection
- 2.3 Evolution within species
- 2.4 The ecology of speciation
- 2.5 Effects of climatic change on the evolution and distribution of species
- 2.6 Effects of continental drift on the ecology of evolution
- 2.7 Interpreting the results of evolution: convergents and parallels

### *Key concepts*

#### KEY CONCEPTS

In this chapter you will:

- appreciate that Darwin and Wallace, who were responsible for the theory of evolution by natural selection, were both, essentially, ecologists
- understand that the populations of a species vary in their characteristics from place to place on both geographic and more local scales, and that some of the variation is heritable
- realize that natural selection can act very quickly on heritable variation – we can study it in action and control it in experiments
- understand that reciprocal transplanting of individuals of a species into each other's habitats can show a finely specialized fit between organisms and their environments
- appreciate that the origin of species requires the reproductive isolation of populations as well as natural selection forcing them to diverge

- realize that natural selection fits organisms to their past – it does not anticipate the future
- realize that the evolutionary history of species constrains what future selection can achieve
- understand that natural selection may produce similar forms from widely different ancestral lines (convergent evolution) or the same range of forms in populations that have become separated (parallel evolution)

*As the great Russian-American biologist Dobzhansky said, 'Nothing in biology makes sense, except in the light of evolution.' But equally, very little in evolution makes sense except in the light of ecology: ecology provides the stage directions through which the 'evolutionary play' is performed. Ecologists and evolutionary biologists need a thorough understanding of each other's disciplines to make sense of key patterns and processes.*

## 2.1 Introduction

The Earth is inhabited by a multiplicity of types of organism. They are distributed neither randomly nor as a homogeneous mixture over the surface of the globe. Any sampled area, even on the scale of a whole continent, contains only a tiny subset of the variety of species present on Earth. Why are there so many types of organism? Why are their distributions so restricted? Answering these ecological questions requires an understanding of the processes of evolution that have led to present-day diversity and distribution.

Until relatively recently, the emphasis with diversity was on using it (for example for medicine), exhibiting it in zoological and botanic gardens, and cataloging it in museums (Box 2.1). Without an understanding of how this diversity developed, such catalogs are more like stamp collecting than science. The enduring contribution of Charles Darwin and Alfred Russel Wallace was to provide ecologists with the scientific foundations to comprehend patterns in diversity and distribution over the face of the Earth.

all species are so specialized that they are almost always absent from almost everywhere

## 2.2 Evolution by natural selection

Darwin and Wallace (Figure 2.1) were both ecologists (although their seminal work was performed before the term was coined) who were exposed to the diversity of nature in the raw. Darwin sailed around the world as naturalist on the 5-year expedition of HMS *Beagle* (1831–36) recording and collecting in the enormous variety of environments that he explored on the way. He gradually developed the view that the natural diversity of nature was the result of a process of evolution

Darwin and Wallace were both ecologists



## 2.1 HISTORICAL LANDMARKS

### 2.1 Historical landmarks

#### A brief history of the study of diversity

An awareness of the diversity of living organisms, and of what lives where, is part of the knowledge that the human species accumulates and hands down through the generations. Hunter–gatherer peoples needed (and still need) detailed knowledge of the natural history of their environments to obtain food successfully and to escape the hazards of being poisoned or eaten. The Arawaks of the South American equatorial forest know where to find and how to catch all the species of large animal around them and also the names of their trees and how they can be used.

Before 2000 BC, the Chinese emperor Shen Nung compiled what was perhaps the first written ‘herbal’ of useful plants and, by the first century AD, Dioscorides had described 500 species of medicinal plants and illustrated many of them.

Collections of living specimens in zoos and gardens also have a long history – certainly back to Greece in the seventh century BC. The urge to collect from the diversity of nature developed in the West in the 17th century when some individuals made their living by finding interesting specimens for other people’s collections. John Tradescant the father (died 1638) and John Tradescant the son (1608–1662) spent most of their lives collecting plants and importing live specimens for the gardens of the British aristocracy. The father was the first English botanist to visit Russia (1618), bringing back many living plants; his son made three visits (1637, 1642 and 1654) to the New World to collect specimens in the American colonies.

Wealthy individuals built up vast collections into personal museums and traveled or sent travelers in search of novelties from new lands as they were discovered and colonized. Naturalists and artists (often the same people) were sent to accompany the major voyages of exploration to report and take home, dead or alive, collections of the diversity of organisms and artefacts that they found. The study of taxonomy and systematics developed and flourished – taxonomy gave names to the various types of organisms; systematics organized and classified them.

When big national museums were established (the British Museum in 1759 and the Smithsonian in Washington in 1846), they were largely compiled from the gifts of personal collections. Like zoos and gardens, the museums’ main role was to make a public display of the diversity of nature, especially the new and curious and rare.

There was no need to explain the diversity – the biblical theory of the 7-day creation of the world sufficed. However, the idea that the diversity of nature had ‘evolved’ over time by progressive divergence from pre-existing stocks was beginning to be discussed around the turn of the 18th and 19th centuries. In 1844 an anonymous publication, *The Vestiges of Creation*, put the cat among the pigeons with a popular account of the idea that animal species had descended from other species.

in which *natural selection* favored some variants within species through a ‘struggle for existence’. He developed this theme over the next 20 years through detailed study and an enormous correspondence with his friends as he prepared a major work for publication with all the evidence carefully marshalled. But he was in no hurry to publish.

In 1858, Wallace wrote to Darwin spelling out, in all its essentials, the same theory of evolution. Wallace was a passionate amateur naturalist. He had read Darwin’s journal of the voyage of the *Beagle* and from 1847 to 1852, with his friend

(a)



(b)

**Figure 2.1**

Photographs of (a) Charles Darwin (lithograph by T. H. Maguire, 1849) and (b) Alfred Russel Wallace (1862).

H.W. Bates, he explored and collected in the river basins of the Amazon and Rio Negro, and from 1854 to 1862 made an extensive expedition in the Malay archipelago. He recalled lying on his bed in 1858 ‘in the hot fit of intermittent fever, when the idea [of natural selection] suddenly came to me. I thought it all out before the fit was over, and . . . I believe I finished the first draft the next day.’

Today, competition for fame and financial support would no doubt lead to fierce conflict about priority – who had the idea first. Instead, in an outstanding example of selflessness in science, sketches of Darwin’s and Wallace’s ideas were presented together at a meeting of the Linnean Society in London. Darwin’s *On the Origin of Species* was then hastily prepared and published in 1859. *On the Origin of Species* may be considered the first major textbook of ecology, and aspiring ecologists would do well to read at least the third chapter.

Both Darwin and Wallace had read *An Essay on the Principle of Population*, published by Malthus in 1798. Malthus’s essay was concerned with the human population, which, if its intrinsic rate of increase remained unchecked, would, he calculated, be capable of doubling every 25 years and overrunning the planet. Malthus realized that limited resources, as well as disease, wars and other disasters, slowed the growth of populations and placed absolute limits on their size. As experienced field naturalists, Darwin and Wallace realized that the Malthusian argument applied with equal force to the whole of the plant and animal kingdoms.

Darwin noted the great fecundity of some species – a single individual of the sea slug *Doris* may produce 600,000 eggs; the parasitic roundworm *Ascaris* may produce 64 million. But he realized that every species ‘must suffer destruction

influence of Malthus’s essay  
on Darwin and Wallace

fundamental truths of  
evolutionary theory

during some period of its life, and during some season or occasional year, otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product.’ In one of the earliest examples of population ecology, Darwin counted all the seedlings that emerged from a plot of cultivated ground 3 feet long and 2 feet wide: “Out of 357 no less than 295 were destroyed, chiefly by slugs and insects”. Both authors, then, emphasized that most individuals die before they can reproduce and contribute nothing to future generations. Both, though, tended to ignore the important fact that those individuals that do survive in a population may leave different numbers of descendants.

The theory of evolution by natural selection, then, rests on a series of established truths:

- 1 Individuals that form a population of a species are not identical.
- 2 Some of the variation between individuals is heritable – that is, it has a genetic basis and is therefore capable of being passed down to descendants.
- 3 All populations could grow at a rate that would overwhelm the environment; but in fact, most individuals die before reproduction and most (usually all) reproduce at less than their maximal rate. Hence, each generation, the individuals in a population are only a subset of those that ‘might’ have arrived there from the previous generation.
- 4 Different ancestors leave different numbers of descendants (descendants, *not* just offspring): they do not all contribute equally to subsequent generations. Hence, those that contribute most have the greatest influence on the heritable characteristics of subsequent generations.

Evolution is the change, over time, in the heritable characteristics of a population or species. Given the above four truths, the heritable features that define a population will inevitably change. Evolution is inevitable.

‘the survival of the fittest’?

But which individuals make the disproportionately large contributions to subsequent generations and hence determine the direction that evolution takes? The answer is: those that were best able to survive the risks and hazards of the environments in which they were born and grew; and those who, having survived, were most capable of successful reproduction. Thus, interactions between organisms and their environments – the stuff of ecology – lie at the heart of the process of evolution by natural selection.

The philosopher Herbert Spencer described the process as ‘the survival of the fittest’, and the phrase has entered everyday language – which is regrettable. First, we now know that survival is only part of the story: differential reproduction is often equally important. But more worryingly, even if we limit ourselves to survival the phrase gets us nowhere. Who are the fittest? – those that survive. Who survives? – those that are fittest. Nonetheless, the term *fitness* is commonly used to describe the success of individuals in the process of natural selection. An individual will survive better, reproduce more and leave more descendants – it will be fitter – in some environments than in others. In a given environment, some individuals will survive better, reproduce more, and leave more descendants – they will be fitter – than other individuals.

Darwin had been greatly influenced by the achievements of plant and animal breeders: for example, the extraordinary variety of pigeons, dogs and farm animals

that had been deliberately bred by selecting individual parents with exaggerated traits. He and Wallace saw nature doing the same thing; 'selecting' those individuals that survived from their excessively multiplying populations: hence the phrase 'natural selection'. But even this phrase can give the wrong impression. There is a great difference between human and natural selection. Human selection has an aim for the future – to breed a cereal with a higher yield, a more attractive pet dog or a cow that will yield more milk. But nature has no aim. Evolution happens because some individuals have survived the death and destruction of the past and reproduced more successfully in the past, not because they were somehow chosen or selected as improvements for the future.

natural selection has no aim for the future

Hence, past environments may be said to have selected particular characteristics of individuals that we see in present-day populations. Those characteristics are 'suited' to present-day environments only because environments tend to remain the same, or at least change only very slowly. We shall see later in this chapter that when environments do change more rapidly, often under human influence, organisms can find themselves, for a time, left 'high and dry' by the experiences of their ancestors.

## 2.3 Evolution within species

The natural world is not composed of a continuum of types of organism each grading into the next: we recognize boundaries between one sort of organism and another. In one of the great achievements of biological science, Linnaeus in 1735 devised an orderly system for naming the different sorts. Part of his genius was to recognize that there were features of both plants and animals that were not easily modified by the organisms' immediate environment, and that these 'conservative' characteristics were especially useful for classifying organisms. In flowering plants, the form of the flowers is particularly stable. Nevertheless, within what we recognize as species, there is often considerable variation, and some of this is heritable. It is on such intraspecific variation, after all, that plant and animal breeders work. In nature, some of this intraspecific variation is clearly correlated with variations in the environment and represents local specialization.

to understand the evolution of species we need to understand evolution within species

Darwin called his book *On the Origin of Species by Means of Natural Selection*, but evolution by natural selection does far more than create new species. Natural selection and evolution occur *within* species, and we now know that we can study them in action and within our own lifetime. Moreover, we need to study the way that evolution occurs within species if we are to understand the origin of new species.

### 2.3.1 Geographic variation within species

Since the environments experienced by a species in different parts of its range are themselves different (to at least some extent), we might expect natural selection to have favored different variants of the species at different sites. But evolution forces the characteristics of populations to diverge from each other (i) only if there is sufficient heritable variation on which selection can act; and (ii) provided that the forces of selection favoring divergence are strong enough to counteract the mixing and hybridization of individuals from different sites.

the characteristics of a species may vary over its geographic range



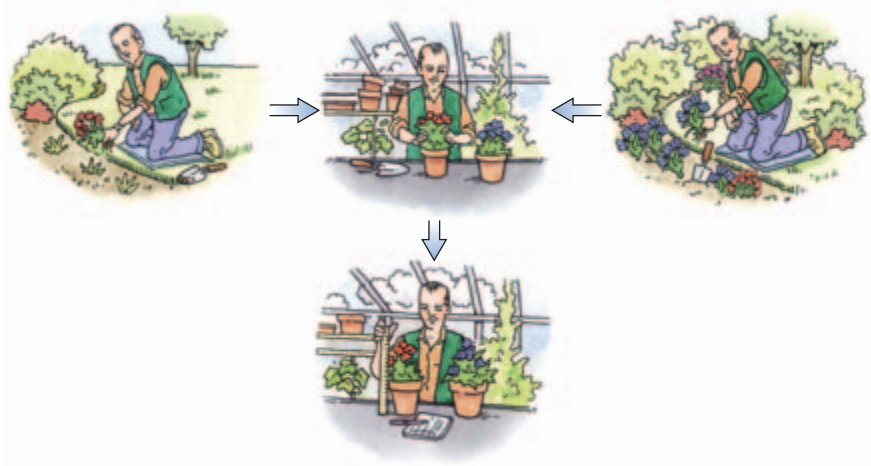
Two populations will not diverge completely if their members (or, in the case of plants, their pollen) are continually migrating between them, mating and mixing their genes.

The sapphire rockcress, *Arabis fecunda*, is a rare perennial herb restricted to calcareous soil outcrops in western Montana – so rare, in fact, that there are just 19 existing populations separated into two groups ('high elevation' and 'low elevation') by a distance of around 100 km. Whether there is local adaptation here is of practical importance: four of the low-elevation populations are under threat from spreading urban areas and may require reintroduction from elsewhere if they are to be sustained. Reintroduction may fail if local adaptation is too marked. Observing plants in their own habitats and checking for differences between them would not tell us if there was local adaptation in the evolutionary sense. Differences may simply be the result of immediate responses to contrasting environments made by plants that are essentially the same. Hence, high- and low-elevation plants were grown together in a 'common garden' (Figure 2.2a),

## Figure 2.2

'Common garden' experiments (a) and reciprocal transplant experiments (b) compare the performance of organisms from different populations of the same species. In the former, organisms are taken from a variety of sources and reared under the same conditions. In the latter, organisms from two (or more) habitats are taken from their own habitat and reared alongside resident organisms in *their* own habitat, in a 'balanced' design such that all organisms are reared in their 'home' habitats and all 'away' habitats.

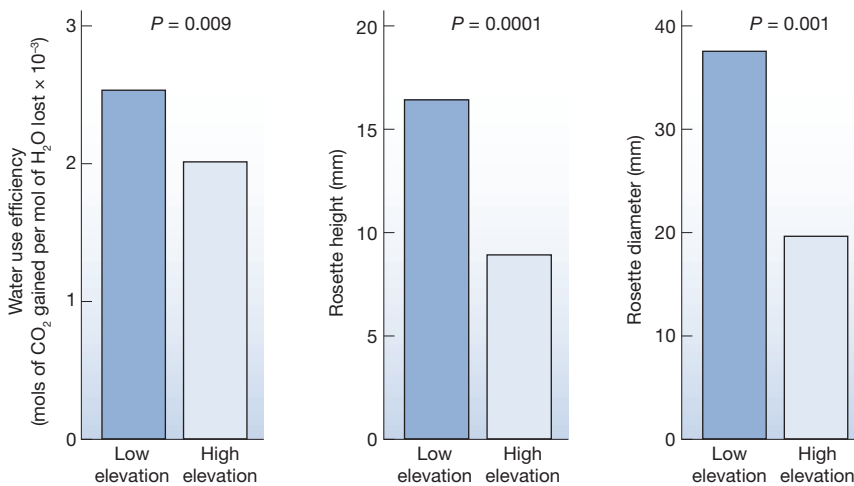
(a) Common garden experiments



(b) Reciprocal transplant experiments





**Figure 2.3**

When plants of the rare sapphire rockcress from low elevation (drought-prone) and high elevation sites were grown together in a common garden, local adaptation was apparent: those from the low elevation site had significantly better water use efficiency as well as having both taller and broader rosettes.

eliminating any influence of contrasting immediate environments. The low-elevation sites were more prone to drought: both the air and the soil were warmer and drier; and the low-elevation plants in the common garden were indeed significantly more drought-tolerant: for example, they had significantly better ‘water use efficiency’ (their rate of water loss through the leaves was low compared to the rate at which carbon dioxide was taken in) as well as being much taller and ‘broader’ (Figure 2.3).

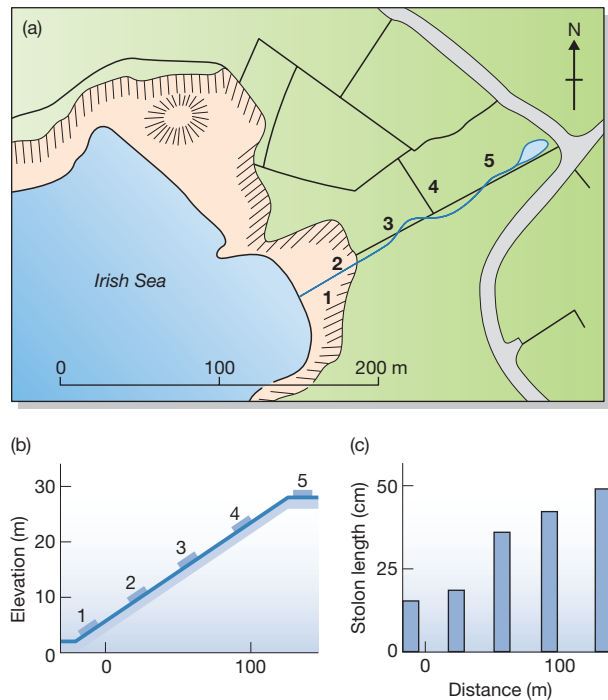
Differentiation over a much smaller spatial scale was demonstrated at a site called Abraham’s Bosom on the coast of North Wales, UK. Here there was an intimate mosaic of very different habitats at the margin between maritime cliffs and grazed pasture, and a common species, creeping bent grass (*Agrostis stolonifera*) was present in many of the habitats. Figure 2.4 shows a map of the site and one of the transects from which plants were sampled; it also shows the results when plants from the sampling points along this transect were grown in a common garden. Each of four plants taken from each sampling point was represented by five rooted clonal replicates of itself. The plants spread by sending out shoots along the ground surface (stolons), and the growth of plants was compared by measuring the lengths of these. In the field, cliff plants formed only short stolons, whereas those of the pasture plants were long. In the experimental garden, these differences were maintained, even though the sampling points were typically only around 30 m apart – certainly within the range of pollen dispersal between plants. Indeed, the gradually changing environment along the transect was matched by a gradually changing stolon length, presumably with a genetic basis, since it was apparent in the common garden. Even over this small scale, the forces of selection seem to outweigh the mixing forces of hybridization.

On the other hand, it would be quite wrong to imagine that local selection always overrides hybridization – that all species exhibit geographically distinct variants with a genetic basis. For example, in a study of *Chamaecrista fasciculata*, an annual legume from disturbed habitats in eastern North America, plants were grown in a common garden that were derived from the ‘home’ site or were transplanted from distances of 0.1, 1, 10, 100, 1000 and 2000 km. Five characteristics were measured: germination, survival, vegetative biomass, fruit production

variation over very short distances

### Figure 2.4

(a) Map of Abraham's Bosom, the site chosen for a study of evolution over very short distances. The green area is grazed pasture; the pale brown area represents cliffs falling to the sea. The numbers indicate sites from which the grass *Agrostis stolonifera* was sampled. Note that the whole area is only 200 m long. (b) A vertical transect across the study area showing gradual change in the numbered sites from pasture to cliff conditions. (c) The mean length of stolons produced in the experimental garden from samples taken from the transect.



FROM ASTON & BRADSHAW, 1966

and the number of fruit produced per seed planted; but for all characters in all replicates there was little or no evidence for local adaptation except at the very farthest spatial scales (e.g. Figure 2.5). There is 'local adaptation' – but it's clearly not *that* local.

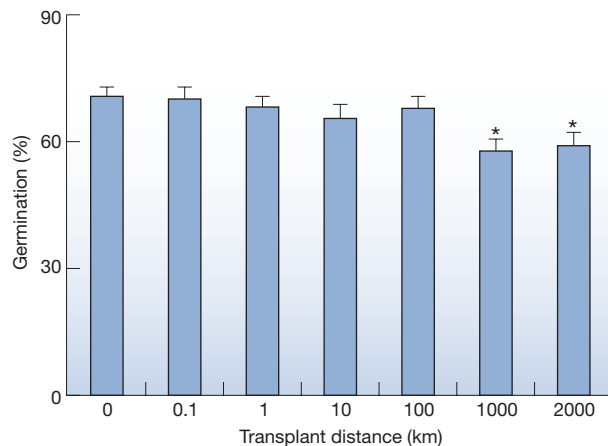
reciprocal transplants test the match between organisms and their environment – e.g. sea anemones transplanted into each other's habitats

We can also test whether organisms have evolved to become specialized to life in their local environment in *reciprocal transplant* experiments (see Figure 2.2b): comparing their performance when they are grown 'at home' (i.e. in their original habitat) with their performance 'away' (i.e. in the habitat of others).

It can be difficult to detect the local specialization of animals by transplanting them into each other's habitat: if they do not like it, most species will run away.

### Figure 2.5

Percentage germination of local (transplant distance zero) and transplanted *Chamaecrista fasciculata* populations to test for local adaptation along a transect in Kansas. Data for 1995 and 1996 have been combined because they do not differ significantly. Populations that differ from the home population at  $P < 0.05$  are indicated by an asterisk. Local adaptation occurs at only the largest spatial scales.



FROM GALLOWAY & FENSTER, 2000

Table 2.1

A reciprocal transplant experiment of the sea anemone *Actinia tenebrosa*. a, b and c are the three replicates in each colony. In each case the proportion of adults that were found brooding young is shown. Transplants back to the home sites are shown in bold print.

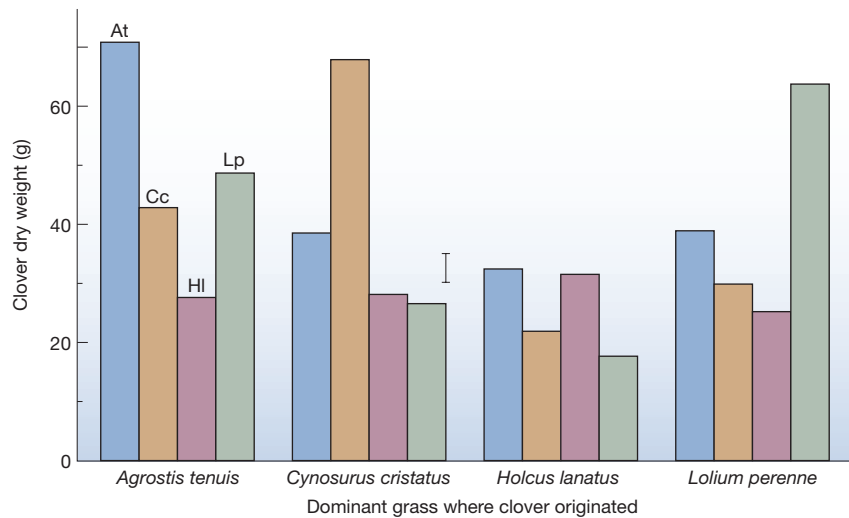
SITE OF ORIGIN	TRANSPLANTED TO SITES AT:		
	GREEN ISLAND	SALMON POINT	STRICKLAND BAY
Green island	a <b>0.42</b>	0.68	0.78
	b <b>0.80</b>	0.63	0.75
	c <b>0.67</b>	0.62	0.61
Salmon Point	a 0.11	<b>0.42</b>	0.13
	b 0.18	<b>0.43</b>	0.28
	c 0.00	<b>0.50</b>	0.40
Strickland Bay	a 0.11	0.06	<b>0.33</b>
	b 0.00	0.06	<b>0.27</b>
	c 0.04	0.20	<b>0.27</b>

But invertebrates like corals and sea anemones are sedentary, and some can be lifted from one place and established in another. The sea anemone *Actinia tenebrosa* is found in pools on headlands around the coast of New South Wales, Australia. Ayre (1985) chose three colonies on headlands within 4 km of each other on which the anemone was abundant. Within each colony, he selected three transplant sites (each 3–5 m long) and at each he set aside three 1 m wide strips – two to receive anemones from the away sites and one to receive ‘transplanted’ individuals from the home site itself. Ayre cleared the experimental sites of all the anemones present and transplanted anemones into them. The number of juveniles brooded per adult was used as a measure of the performance of the anemones home and away.

The proportion of adults that were found brooding 11 months later is shown in Table 2.1. Anemones originally sampled from Green Island were rather successful in brooding young after being transplanted both home and away and did not show any specialization to their home environment. However, in all the other transplant experiments a greater proportion of anemones brooded young at home than at away sites: strong evidence of evolved local specialization. In later experiments, Ayre (1995) lifted anemones from a variety of sites as before, but he then kept them for a period to acclimate at a common site before transplanting them in a reciprocal experiment. This more severe test convincingly confirmed the results in Table 2.1.

Another reciprocal transplant experiment was carried out with white clover (*Trifolium repens*), which forms clones in grazed pastures. To determine whether the characteristics of individual clones matched local features of their environment, Turkington and Harper (1979) removed plants from marked positions in the field and multiplied them into clones in the common environment of a greenhouse. They then transplanted plants from each clone into the place in the vegetation from which it had originally been taken, and also to the places from

a reciprocal transplant experiment involving a plant



**Figure 2.6**

Plants of white clover (*Trifolium repens*) were sampled from a field of permanent grassland from local patches dominated by four different species of grass: *Agrostis tenuis* (At), *Cynosurus cristatus* (Cc), *Holcus lanatus* (HI), and *Lolium perenne* (Lp). The clover plants were multiplied into clones and transplanted (in all possible combinations) into plots that had been sown individually with seeds of each of the four grass species. The histograms show the average weights of the transplanted white clover after 12 months' growth. The vertical bar indicates the difference between the height of any pair of columns that is statistically significant at  $P < 0.05$ . Note, in the panel of four histograms on the left, how clover that came originally from a patch of *Agrostis tenuis* grew significantly better in the presence of this grass (At) than any of the other species (Cc, HI, Lp). Equivalent patterns are evident for clover that originated from patches of *Cynosurus cristatus* and *Lolium perenne* (strongest clover growth with Cc and Lp, respectively). Clover from *Holcus lanatus* patches did not follow the general trend, growing as well with At as with HI.

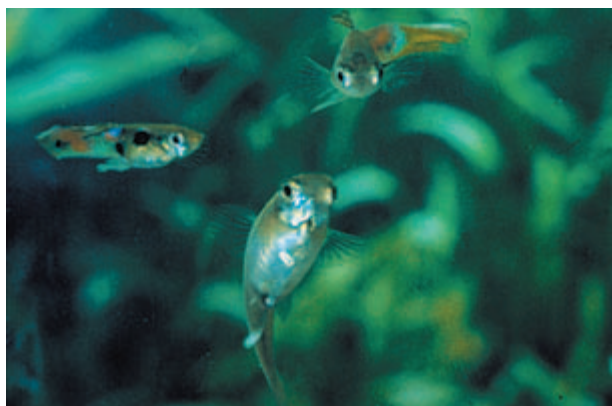
FROM TURKINGTON & HARPER, 1979

where all the others had been taken. The plants were allowed to grow for a year before they were removed, dried and weighed. The mean weight of clover plants transplanted back into their home sites was 0.89 g but at away sites it was only 0.52 g, a statistically highly significant difference.

The clover plants had been chosen from patches dominated by four different species of grass. Hence, in a second experiment, samples from the different clones were planted into dense experimental plots of the four grasses (Figure 2.6). The mean yield of clovers grown with their original neighbor grass was 59.4 g; the mean yield with 'alien' grasses was 31.9 g, again a highly significant difference. Thus, clover clones in the pasture had evolved to become specialized such that they tended to perform best (make most growth) in their local environment and with their local neighbors.

In most of the examples so far, geographic variants of species have been identified, but the selective forces favoring them have not. This is not true of the next example. The guppy (*Poecilia reticulata*), a small freshwater fish from north-eastern South America, has been the material for a classic series of evolutionary experiments. In Trinidad, many rivers flow down the northern range of mountains and are subdivided by waterfalls that isolate fish populations above the falls from those below. Guppies are present in almost all these water bodies, and

natural selection by predation:  
a controlled field experiment  
in fish evolution

**Figure 2.7**

Male and female guppies (*Poecilia reticulata*) showing two flamboyant males courting a typical, dull-colored female.

in the lower waters they meet various species of predatory fish that are absent higher up the rivers. The populations of guppies in Trinidad differ from each other in almost every feature that biologists have examined. Forty-seven of these traits tend to vary in step with each other (they *covary*) and with the intensity of the risk from predators. This correlation suggests that the guppy populations have been subject to natural selection from the predators. But the fact that two phenomena are correlated does not prove that one causes the other. Only controlled experiments can establish cause and effect.

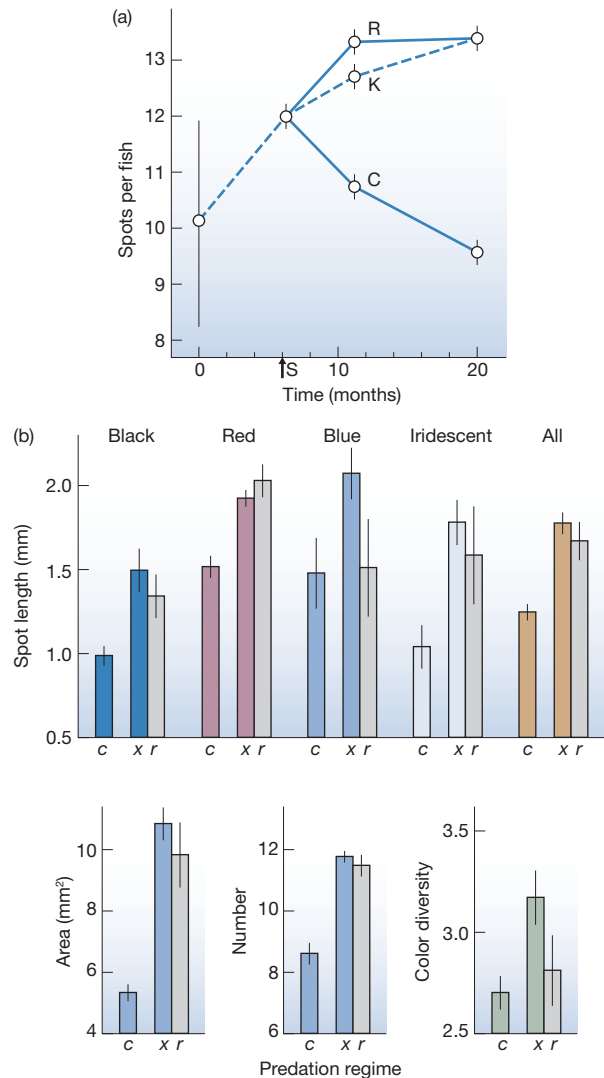
Where guppies have been free or relatively free from predators, the males are brightly decorated with different numbers and sizes of colored spots (Figure 2.7). Females are dull and dowdy and (at least, to us) inconspicuous. Whenever we study natural selection in action, it becomes clear that compromises are involved. For every selective force that favors change, there is a counteracting force that resists the change. Color in male guppies is a good example. Female guppies prefer to mate with the most gaudily decorated males – but these are more readily captured by predators because they are easier to see.

This sets the stage for some revealing experiments on the ecology of evolution. Guppy populations were established in ponds in a greenhouse and exposed to different intensities of predation. The number of colored spots per guppy fell sharply and rapidly when the population suffered heavy predation (Figure 2.8a). Then, in a field experiment, 200 guppies were moved from a site far down the Aripo River where predators were common and introduced to a site high up the river where there were neither guppies *nor* predators. The transplanted guppies thrived in their new site, and within just 2 years the males had more and bigger spots of more varied color (Figure 2.8b). The females' choice of the more flamboyant males had dramatic effects on the gaudiness of their descendants, but this was only because predators were not present to reverse the direction of selection.

The speed of evolutionary change in this experiment in nature was as fast as that in artificial selection experiments in the laboratory. Many more fish were produced than would eventually survive (as many as 14 generations of fish occurred in the 23 months during which the experiment took place) and there was considerable genetic variation in the populations upon which natural selection could act.

**Figure 2.8**

(a) An experiment showing changes in populations of guppy *Poecilia reticulata* exposed to predators in experimental ponds. The graph shows changes in the number of colored spots per fish in ponds with different populations of predatory fish. The initial population was deliberately collected from a variety of sites so as to display high variability and was introduced to the ponds at time 0. At time S, weak predators (*Rivulus hartii*) were introduced to ponds R, a high intensity of predation by the dangerous predator *Crenicichila alta* was introduced into ponds C, while ponds K continued to contain no predators (the vertical lines show  $\pm 2$  SE). The number of spots per fish declined in treatments with the dangerous predator, but increased in the absence of fish or the presence of weak predators. (b) Results of a field experiment. A population of guppies originating in a locality with dangerous predators (*c*) was transferred to a stream having only the weak predator (*Rivulus hartii*) and, until the introduction, no guppies (*x*). Another stream nearby with guppies and *R. hartii* served as a control (*r*). The results shown are from guppies collected at the three sites 2 years after the introductions. Note how *x* and *r*, the sites with only weak predation, have converged and thus how *x* has changed dramatically from the source population with dangerous predators, *c*. In the absence of strong predators, the size, number and diversity of colored spots increased significantly within 2 years.

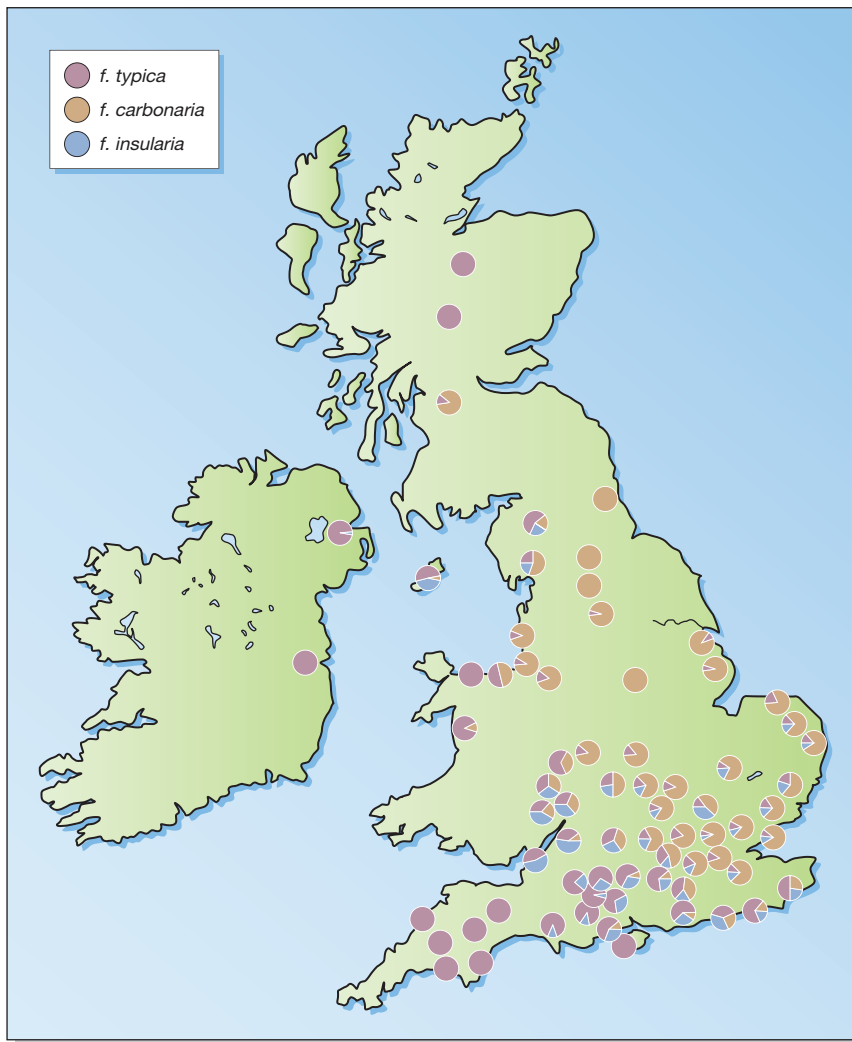


AFTER ENDLER, 1980

### 2.3.2 Variation within a species with manmade selection pressures

natural selection by pollution – the evolution of a melanic moth

It is not surprising that some of the most dramatic examples of natural selection in action have been driven by the ecological forces of environmental pollution – these can provide rapid change under the influence of powerful selection pressures. Pollution of the atmosphere in and after the Industrial Revolution has left evolutionary fingerprints in the most unlikely places. *Industrial melanism* is the phenomenon in which black or blackish forms of species of moths and other organisms have come to dominate populations in industrial areas. In the dark individuals, a dominant gene is responsible for producing an excess of the black pigment melanin. Industrial melanism is known in most industrialized countries, including some parts of the United States (e.g. Pittsburgh), and more than 100 species of moth have evolved forms of industrial melanism.

**Figure 2.9**

Sites in Britain and Ireland where the frequencies of the pale (*forma typica*) and melanic forms of *Biston betularia* were recorded by Kettlewell and his colleagues. In all more than 20,000 specimens were examined. The principal melanic form (*forma carbonaria*) was abundant near industrial areas and where the prevailing westerly winds carry atmospheric pollution to the east. A further melanic form (*forma insularia*, which looks like an intermediate form but is due to several different genes controlling darkening) was also present but could not be detected where the genes for *forma carbonaria* were present.

FROM FORD, 1975

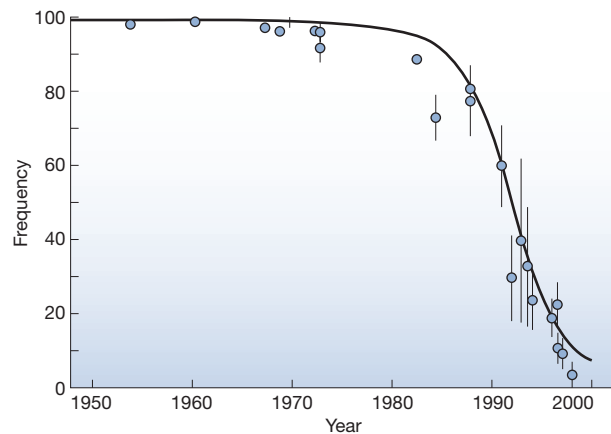
The earliest recorded species to evolve in this way was the peppered moth (*Biston betularia*); the first black specimen was caught in Manchester, UK in 1848. By 1895, about 98% of the Manchester peppered moth population was melanic. Following many more years of pollution, a large-scale survey of pale and melanic forms of the peppered moth in Britain recorded more than 20,000 specimens between 1952 and 1970 (Figure 2.9). The winds in Britain are predominantly westerlies, spreading industrial pollutants (especially smoke and sulfur dioxide) toward the east. Melanic forms were concentrated toward the east and were completely absent from unpolluted western parts of England and Wales, northern Scotland, and Ireland.

The moths are preyed upon by insectivorous birds that hunt by sight. In a field experiment, large numbers of melanic and pale ('typical') moths were reared and released in equal numbers in a rural and largely unpolluted area of southern England. Of the 190 moths that were captured by birds, 164 were melanic and



**Figure 2.10**

Change in the frequency of the *carbonaria* form of the peppered moth *Biston betularia* in the Manchester area since 1950, covering the period where smoke pollution has been controlled and the frequency has declined dramatically. Vertical lines show standard errors.



AFTER COOK ET AL., 1999

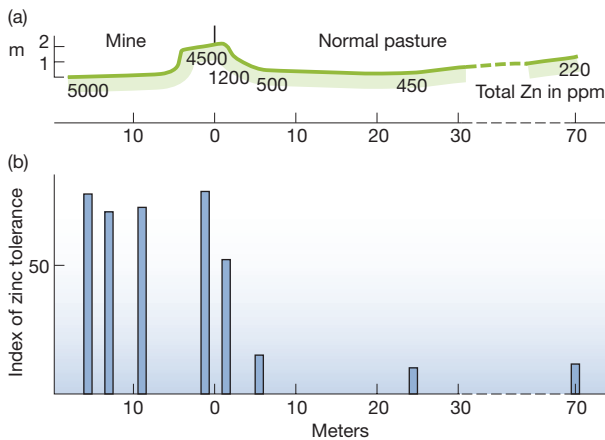
26 were typicals. An equivalent study was made in an industrial area near the city of Birmingham. Twice as many melanics as typicals were recaptured. This showed that a significant selection pressure was exerted through bird predation, and that moths of the typical form were clearly at a disadvantage in the polluted industrial environment (where their light color stood out against a sooty background), whereas the melanic forms were at a disadvantage in the pollution-free countryside (Kettlewell, 1955).

In the 1960s, however, industrialized environments in Western Europe and the United States started to change as oil and electricity began to replace coal, and legislation was passed to impose smoke-free zones and to reduce industrial emissions of sulfur dioxide (see Chapter 13). The frequency of melanic forms then fell back to near preindustrial levels with remarkable speed (Figure 2.10).

The forces of selection at work, first in favor of and then against melanic forms, have clearly been related to industrial pollution, but the idea that melanic forms were favored simply because they were camouflaged against smoke-stained backgrounds may be only part of the story. The moths rest on tree trunks during the day, and non-melanic moths are well hidden against a background of mosses and lichens. Industrial pollution had not just blackened the moths' background; atmospheric pollution, especially  $\text{SO}_2$ , had also destroyed most of the moss and lichen on the tree trunks. Indeed the distribution of melanic forms in Figure 2.9 closely fits the areas in which tree trunks were likely to have lost lichen cover as a result of  $\text{SO}_2$  and so ceased to provide such effective camouflage for the non-melanic moths. Thus  $\text{SO}_2$  pollution may have been as important as smoke in selecting melanic moths.

Some plants are tolerant of another form of pollution: the presence of toxic heavy metals such as lead, zinc, and copper, which contaminate the soil after mining. Populations of plants on contaminated areas may be tolerant, while at the edge of these areas a transition from tolerant to intolerant forms can occur over very short distances (Figure 2.11). In some cases it has been possible to measure the speed of evolution. Zinc-tolerant forms of two species of the grass *Agrostis capillaris* were found to have evolved under zinc-galvanized electricity pylons within 20–30 years of their erection (Al-Hiyaly et al., 1988).

natural selection by pollution –  
evolution of heavy-metal  
tolerance in plants

**Figure 2.11**

The grass *Anthoxanthum odoratum* colonizes land heavily contaminated with zinc (Zn) on old mines. This is possible because the grass has evolved zinc-tolerant forms. (a) Samples of the grass were taken along a transect from a mine (at Trelogan in North Wales) into surrounding grassland (zinc concentrations in the soil are shown as parts per million, ppm) and were tested for zinc tolerance by measuring the length of roots that they produced when grown in a culture solution containing excess zinc. (b) The index of zinc tolerance falls off steeply over a distance of 2–5 m at the mine boundary.

### 2.3.3 Evolution and coevolution

It is easy to see that a population of plants faced with repeated drought is likely to evolve a tolerance of water shortage, and an animal repeatedly faced with cold winters is likely to evolve habits of hibernation or a thick protective coat. But droughts do not become any less severe as a result, nor winters milder. Physical conditions are not heritable: they leave no descendants, and they are not subject to natural selection. But the situation is quite different when two species interact: predator on prey, parasite on host, competitive neighbor on neighbor. Natural selection may select from a population of parasites those that are more efficient at infecting their host. But this immediately sets in play forces of natural selection that favor more resistant hosts. As they evolve, they put further pressure on the ability of the parasite to infect. Host and parasite are then caught in never-ending reciprocating selection: they *coevolve*. In many other ecological interactions, the two parties are not antagonists but positively beneficial to one another: *mutualists*. Pollinators and their plants, and leguminous plants and their nitrogen-fixing bacteria, are well-known examples. We consider coevolution in some detail when we return to more evolutionary aspects of ecology in Chapter 8.

## 2.4 The ecology of speciation

We have seen that natural selection can force populations of plants and animals to change their character – to evolve. But none of the examples we have considered has involved the evolution of a new species. Indeed Darwin's *On the Origin of Species* is about natural selection and evolution but is not really about the origin of species! 'Black' and 'typical' peppered moths are forms within a species, not different species. Likewise, the different growth forms of the grasses on the cliffs and pastures of Abraham's Bosom and the dull and flamboyant races of guppies are just local genetic classes. None qualifies for the status of distinct species. But when we ask just what criteria justify naming two populations as different species we meet real problems.

### 2.4.1 What do we mean by a 'species'?

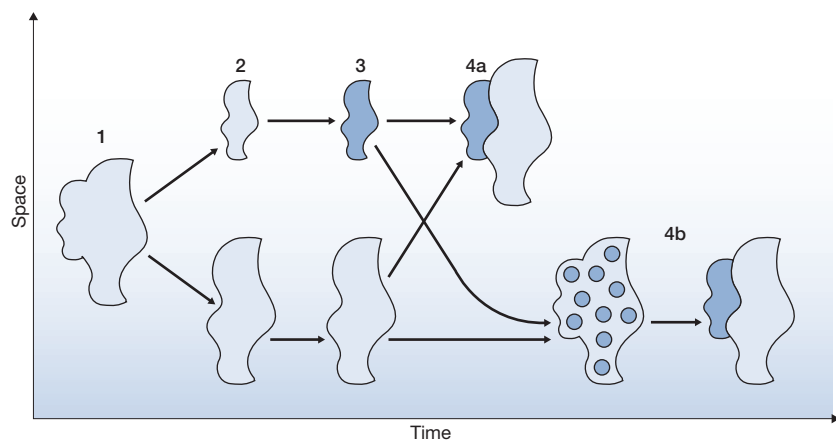
Cynics have said, with some truth, that a species is what a competent taxonomist regards as a species. Darwin himself regarded species (like genera) as 'merely artificial combinations made for convenience'. On the other hand, in the 1930s, two American biologists, Mayr and Dobzhansky, proposed an empirical test that could be used to decide whether two populations were part of the same species or of two different species. They recognized organisms as being members of a single species if they could, at least potentially, breed together in nature to produce fertile offspring. They called a species tested and defined in this way a *biospecies*. In the examples that we have used earlier in this chapter we know that melanic and normal peppered moths can mate and that the offspring are fully fertile; this is also true of colored and dull guppies and of plants from the different types of *Agrostis*. They are all variations within species – not separate species.

biospecies do not exchange genes

In practice, however, biologists do not apply the Mayr–Dobzhansky test before they recognize every species: there is simply not enough time and resources. What is more important is that the test recognizes a crucial element in the evolutionary process. Two parts of a population can evolve into distinct species only if some sort of barrier prevents gene flow between them. If the members of two populations are able to hybridize and their genes are combined and reassorted in their progeny, then natural selection can never make them truly distinct.

orthodox speciation

The most orthodox scenario for speciation comprises a number of stages (Figure 2.12). First, two subpopulations become geographically isolated and natural selection drives genetic adaptation to their local environments. Next, as a *byproduct* of this genetic differentiation, a degree of reproductive isolation builds



**Figure 2.12**

The orthodox picture of ecological speciation. A uniform species with a large range (1) differentiates into subpopulations (2; for example, separated by geographic barriers or dispersed onto different islands), which become genetically isolated from each other (3). After evolution in isolation they may meet again, when they are either already unable to hybridize (4a) and have become true biospecies, or they produce hybrids of lower fitness (4b), in which case evolution may favor features that prevent interbreeding between the 'emerging species' until they are true biospecies.

up between the two. This may be, for example, a difference in courtship ritual, tending to prevent mating in the first place. This is referred to as 'prezygotic' isolation. Alternatively, the offspring themselves may simply display a reduced viability. Then, in a phase of *secondary contact*, the two subpopulations re-meet. The hybrids between individuals from the different subpopulations are now of low fitness, because they are literally neither one thing nor the other. Natural selection will then favor any feature in either subpopulation that *reinforces* reproductive isolation, especially prezygotic characteristics, preventing the production of low-fitness hybrid offspring. These breeding barriers then cement the distinction between what have now become separate species.

It would be wrong, however, to imagine that all examples of speciation conform fully to this orthodox picture (Schluter, 2001). First, there may never be secondary contact. This would be pure 'allopatric' speciation (that is, with all divergence occurring in subpopulations in *different* places). This is especially likely for island species, which are examined further below.

Second, there has been increasing support for the view that a phase of physical isolation is not necessary: that is, '*sympatric*' speciation is possible (divergence occurring in subpopulations in the *same* place). One circumstance in which this seems likely to occur is where insects feed on more than one species of host plant, and where each requires specialization by the insects to overcome the plant's defenses. (Consumer-resource defense and specialization are examined more fully in Chapters 3 and 7.) Particularly persuasive in this is the existence of a continuum from populations of insects feeding on more than one host plant, through populations differentiated into 'host races' (coexisting subpopulations that specialize on different host plants but exchange genes at a rate of more than around 1% per generation), to distinct but closely related coexisting species, specializing on their particular hosts (Drès and Mallet, 2001). This continuum reminds us that the origin of a species, whether allopatric or sympatric, is a process, not an event. For the formation of a new species, like the boiling of an egg, there is some freedom to argue about when it is completed.

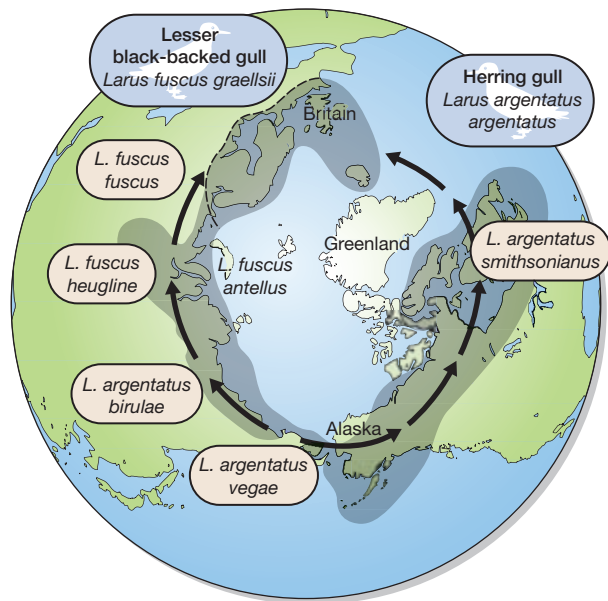
These same points are further illustrated by the extraordinary case of two species of sea gull. The lesser black-backed gull (*Larus fuscus*) originated in Siberia and colonized progressively to the west, forming a chain or *cline* of different forms, spreading from Siberia to Britain and Iceland (Figure 2.13). The neighboring forms along the cline are distinctive, but they hybridize readily in nature. Neighboring populations are therefore regarded as part of the same species and taxonomists give them only 'subspecific' status (e.g., *Larus fuscus graelsii*, *Larus fuscus fuscus*, the three words referring to genus, species and subspecies). Populations of the gull have, however, also spread east from Siberia, again forming a cline of freely hybridizing forms. Together, the populations spreading east and west encircle the northern hemisphere. They meet and overlap in northern Europe. There, the eastward and westward clines have diverged so far that it is easy to tell them apart, and they are recognized as two different *species*, the lesser black-backed gull (*Larus fuscus*) and the herring gull (*Larus argentatus*). Moreover, the two species do not hybridize: they have become true biospecies. We can see how two distinct species have evolved from one primal stock, and that the stages of their divergence remain frozen in the cline that connects them.

allopatric and sympatric  
speciation

evolution in sea gulls

**Figure 2.13**

Two species of gull, the herring gull and the lesser black-backed gull, have diverged from a common ancestry as they have colonized and encircled the northern hemisphere. Where they occur together in northern Europe they fail to interbreed and are clearly recognized as two distinct species. However, they are linked along their ranges by a series of freely interbreeding races or subspecies.



AFTER BROOKES, 1998

## 2.4.2 Islands and speciation

### Darwin's finches

It is, though, when a population becomes split into completely isolated populations, dispersed onto different islands especially, that they most readily diverge into distinct species. The most celebrated example of evolution and speciation on islands is the case of Darwin's finches in the Galapagos archipelago. The Galapagos are volcanic islands isolated in the Pacific Ocean about 1000 km west of Ecuador and 750 km from the island of Cocos, which is itself 500 km from Central America. At more than 500 m above sea level the vegetation is open grassland. Below this is a humid zone of forest that grades into a coastal strip of desert vegetation with some endemic species of prickly pear cactus (*Opuntia*). Fourteen species of finch are found on the islands, and there is every reason to suppose that these evolved from a single ancestral species that invaded the islands from the mainland of Central America.

In their remote island isolation, the Galapagos finches have radiated into a variety of species in groups with contrasting ecologies (Figure 2.14). Members of one group, including *Geospiza fuliginosa* and *G. fortis*, have strong bills and hop and scratch for seeds on the ground. *Geospiza scandens* has a narrower and slightly longer bill and feeds on the flowers and pulp of the prickly pears as well as on seeds. Finches of a third group have parrot-like bills and feed on leaves, buds, flowers and fruits, and a fourth group with a parrot-like bill (*Camarhynchus psittacula*) has become insectivorous, feeding on beetles and other insects in the canopy of trees. A so-called woodpecker finch, *Camarhynchus (Cactospiza) pallida*, extracts insects from crevices by holding a spine or a twig in its bill. Yet a further group includes a species (*Certhidea olivacea*) that, rather like a warbler, flits around actively and collects small insects in the forest canopy and in the air. Populations of ancestor species became reproductively isolated, most likely after chance colonization of different islands within the archipelago, and evolved

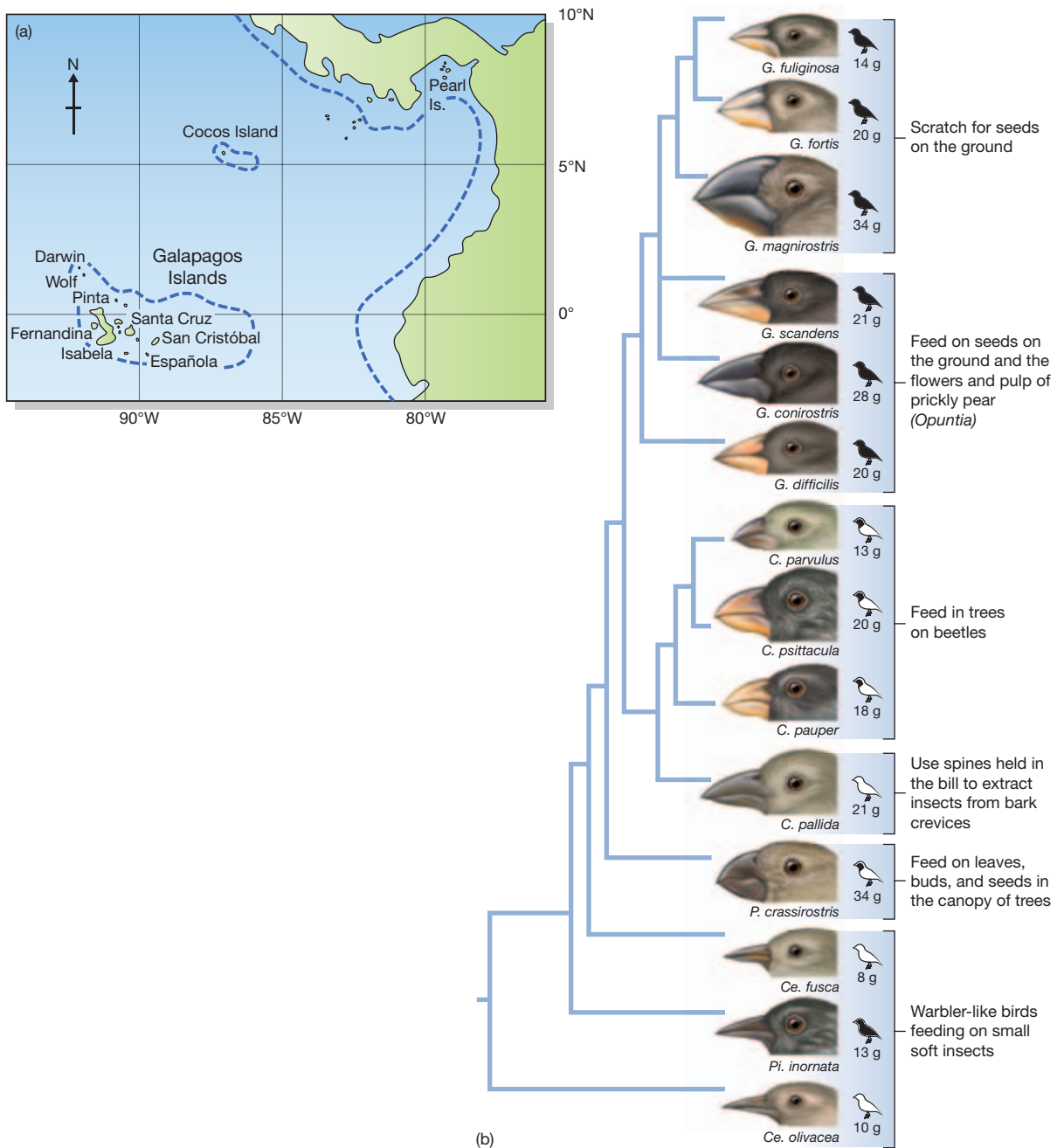


Figure 2.14

(a) Map of the Galapagos Islands showing their position relative to Central and South America; on the equator 5° equals approximately 560 km. (b) A reconstruction of the evolutionary history of the Galapagos finches based on variation in the length of microsatellite DNA. The *genetic distance* (a measure of the genetic difference) between species is shown by the length of the horizontal lines. Notice the great and early separation of the warbler finch (*Certhidea olivacea*) from the others, suggesting that it may closely resemble the founders that colonized the islands. The feeding habits of the various species are also shown. Drawings of the birds are proportional to actual body size. The maximum amount of black coloring in male plumage and the average body mass are shown for each species. *C.*, *Camarhynchus*; *Ce.*, *Certhidea*; *G.*, *Geospiza*; *P.*, *Platyspiza*; *Pi.*, *Pinaroloxias*.

separately for a time. Subsequent movements between islands may have brought non-hybridizing biospecies together, and subsequently these have evolved to fill different niches. We will see in Chapter 6 that when individuals from different species compete, natural selection may act to favor those individuals that compete least with members of the other species. An expected consequence is that among a group of closely related species, such as Darwin's finches, differences in feeding and other aspects of their ecology are likely to become enhanced with time.

The evolutionary relationships among the various Galapagos finches have been traced by molecular techniques (analyzing variation in 'microsatellite' DNA; Petren et al., 1998) (Figure 2.14). These accurate modern tests confirm the long-held view that the family tree of the Galapagos finches radiated from a single trunk (i.e. was *monophyletic*) and also provides strong evidence that the warbler finch (*Certhidea olivacea*) was the first to split off from the founding group and is likely to be the most similar to the original colonist ancestors. The entire process of evolutionary divergence of these species appears to have happened in less than 3 million years.

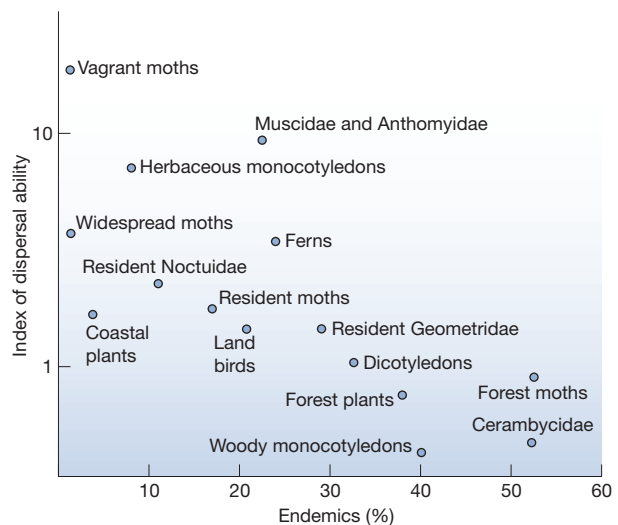
#### island endemics

The flora and fauna of many other archipelagos show similar examples of great richness of species with many local *endemics* (i.e. species known only from one island or area). Lizards of the genus *Anolis* have evolved a kaleidoscopic diversity of species on the islands of the Caribbean; and isolated groups of islands, such as the Canaries off the coast of North Africa, are treasure troves of endemic plants. The endemics evolve, of course, because they are isolated from individuals of the original species, or other species, with which they might hybridize. An illustration of the importance of isolation in the evolution of endemics is provided by the animals and plants of Norfolk Island. This small island (about 70 km<sup>2</sup>) is approximately 700 km from New Caledonia and New Zealand, but about 1200 km from Australia. Hence, the ratio of Australian species to New Zealand and New Caledonian species within a group can be used as a measure of that group's dispersal ability, and the poorer the dispersal ability the greater the isolation. As Figure 2.15 shows, the proportion of endemics on Norfolk Island is highest in groups with poor dispersal ability (more isolated) and lowest in groups with good dispersal ability.

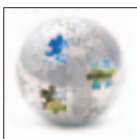
Unusual and often rich communities of endemics may also pose particular problems for the applied ecologist (Box 2.2).

### Figure 2.15

The evolution of endemic species on islands as a result of their isolation from individuals of an original species with which they might interbreed. Poorly dispersing (and therefore more 'isolated') groups on Norfolk Island have a higher proportion of endemic species and are more likely to contain species from either New Caledonia or New Zealand than from Australia, which is further away.







## 2.2 TOPICAL ECOncerns

### Deep sea vent communities at risk

Deep sea vents are islands of warmth in oceans that are otherwise cold and inhospitable. As a consequence, they support unique communities, rich in endemic species. One of the latest controversies to pit environmentalists against industrialists concerns these deep sea vents, which are also now known to be sites rich in minerals. This newspaper article by William J. Broad appeared in the *San Jose Mercury News*, January 20, 1998.

With miners staking claim to valuable metals lying in undersea lodes in the South Pacific, questions surface about how to prevent disasters in these fragile, little understood ecosystems.

The volcanic hot springs of the deep sea are dark oases that teem with blind shrimp, giant tube worms and other bizarre creatures, sometimes in profusions great enough to rival the chaos of rain forests. And they are old.

Scientists who study them say these odd environments, first discovered two decades ago, may have

been the birthplace of all life on Earth, making them central to a new wave of research on evolution.

Now, in a moment that diverse ranks of experts have feared and desired for years, miners are invading the hot springs, possibly setting the stage for the last great battle between industrial development and environmental preservation.

The undersea vents are rich not just in life but in valuable minerals such as copper, silver and gold. Indeed, their smoky chimneys and rocky foundations are virtual foundries for precious metals. . . . The fields of undersea gold have long fired the imaginations of many scientists and economists, but no mining took place, in part because the rocky deposits were hard to lift from depths of a mile or more.

Now, however, miners have staked the first claim to such metal deposits after finding the richest ores ever. The estimated value of copper, silver and gold at a South Pacific site is up to billions of dollars. Environmentalists, though, want to protect the exotic ecosystem by banning or severely limiting mining.

(Article written for the *New York Times*. Copyright Globe Newspaper Company; reprinted by permission.)



A deep sea vent community.

© WHOI, J. EDMOND, VISUALS UNLIMITED

Consider the following options and debate their relative merits:

- 1 Allow the mining industry free access to all deep sea vents, since the wealth created will benefit many people.
- 2 Ban mining and other disruption of all deep sea vent communities, recognizing their unique biological and evolutionary characteristics.
- 3 Carry out biodiversity assessments of known vent communities and prioritize according to their conservation importance, permitting mining in cases that will minimize overall destruction of this category of community.

## 2.5 Effects of climatic change on the evolution and distribution of species

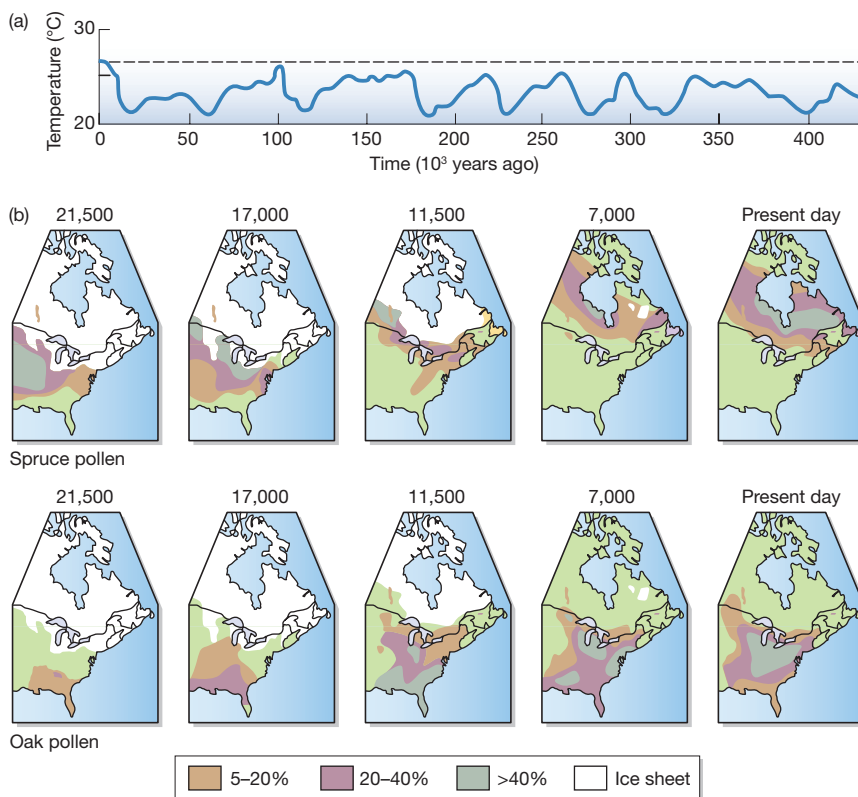
Changes in climate, particularly during the ice ages of the Pleistocene (the past 2–3 million years), bear a lot of the responsibility for the present patterns of distribution of plants and animals. As climates have changed, species populations have advanced and retreated, have been fragmented into isolated patches, and may have then rejoined. Much of what we see in the present distribution of species represents phases in a recovery from past climatic change. Modern techniques for analyzing and dating biological remains (particularly buried pollen) are beginning to allow us to detect just how much of the present distribution of organisms is a precise, local, evolved match to present environments, and how much is a fingerprint left by the hand of history.

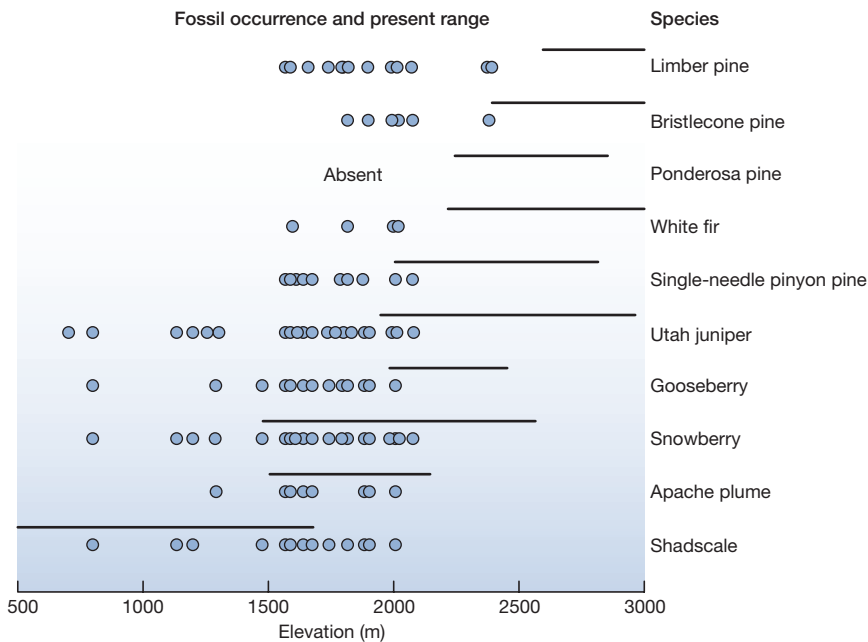
For most of the past 2–3 million years the Earth has been very cold. Evidence from the distribution of oxygen isotopes in cores taken from the deep ocean floor shows that there may have been as many as 16 glacial cycles in the Pleistocene, each lasting for up to 125,000 years (Figure 2.16a). Each cold (glacial) phase may have lasted for as long as 50,000–100,000 years, with brief intervals of only 10,000–20,000 years when the temperatures rose to, or above, those of today. In this case, present floras and faunas are unusual, having developed at the warm end of one of a series of unusual catastrophic warm periods.

cycles of glaciation have occurred repeatedly

**Figure 2.16**

(a) An estimate of the global temperature variations with time during glacial cycles over the past 400,000 years. The estimates were obtained by comparing oxygen isotope ratios in fossils taken from ocean cores in the Caribbean. The dashed line corresponds to the ratio 10,000 years ago, at the start of the present warming period. Periods as warm as the present have been rare events, and the climate during most of the past 400,000 years has been glacial. (b) Ranges in eastern North America, as indicated by pollen percentages in sediments, of spruce species (above) and oak species (below) from 21,500 years ago to the present. Note how the ice sheet contracted during this period.



**Figure 2.17**

The elevation ranges of 10 species of woody plant from the mountains of the Sheep Range, Nevada during the last glaciation (dots) and at present (solid line).

During the 20,000 years since the peak of the last glaciation, global temperatures have risen by about 8°C. The analysis of buried pollen – particularly of woody species, which produce most of the pollen – can show how vegetation has changed during this period (Figure 2.16b). As the ice retreated, different forest species advanced in different ways and at different speeds. For some, like the spruce of eastern North America, there was displacement to new latitudes; for others, like the oaks, the picture was more one of expansion.

We do not have such good records for the postglacial spread of the animals associated with the changing forests, but it is at least certain that many species could not have spread faster than the trees on which they feed. Some of the animals may still be catching up with their plants, and tree species are still returning to areas they occupied before the last ice age! It is quite wrong to imagine that our present vegetation is in some sort of equilibrium with (adapted to) the present climate.

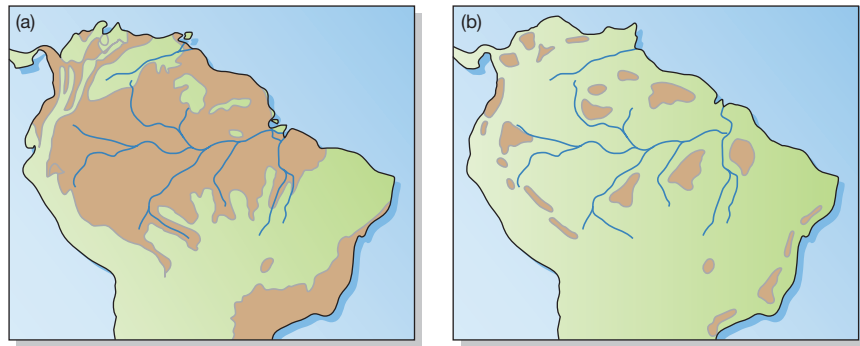
Even in regions that were never glaciated, pollen deposits record complex changes in distribution: in the mountains of the Sheep Range, Nevada, for example, woody species show different patterns of change in elevational range (Figure 2.17). The species composition of vegetation has continually been changing and is almost certainly still doing so.

The records of climatic change in the tropics are far less complete than those for temperate regions. Many believe, though, that during cooler, drier glacial periods, the tropical forests retreated to smaller patches, surrounded by a sea of savanna. Support for this comes from the present-day distribution of species in the tropical forests of South America (Figure 2.18). There, particular ‘hotspots’ of species diversity are apparent, and these are thought to be likely sites of forest refuges during the glacial periods, and sites too, therefore, of increased rates of speciation (Ridley, 1993). On this interpretation, the present distributions of

the distribution of trees has changed gradually since the last glaciation

**Figure 2.18**

(a) The present-day distribution of tropical forest in South America.  
 (b) The possible distribution of tropical forest refuges at the time when the last glaciation was at its peak, as judged by present-day hot spots of species diversity within the forest.



predicted global warming by the 'greenhouse effect' is nearly 100 times faster than postglacial warming

species may again be seen as largely accidents of history (where the refuges were) rather than precise matches between species and their differing environments.

Evidence of changes in vegetation that followed the last retreat of the ice hint at the likely consequences of the global warming (maybe 3°C in the next 100 years) that is predicted to result from continuing increases in 'greenhouse' gases in the atmosphere (see Chapter 13). But the scales are quite different. Postglacial warming of about 8°C occurred over around 20,000 years, and changes in the vegetation failed to keep pace even with this. But current projections for the 21st century require range shifts for trees at rates of 300–500 km per century compared to typical rates in the past of 20–40 km per century (and exceptional rates of 100–150 km). It is striking that the only precisely dated extinction of a tree species in the Quaternary period, that of *Picea critchfeldii*, occurred around 15,000 years ago at a time of especially rapid postglacial warming (Jackson & Weng, 1999). Clearly, even more rapid change in the future could result in extinctions of many additional species (Davis & Shaw, 2001).

## 2.6 Effects of continental drift on the ecology of evolution

land masses have moved . . .

The patterns of species formation that occur on islands appear on an even larger scale in the evolution of genera and families across continents. Many curious distributions of organisms between continents seem inexplicable as the result of dispersal over vast distances. Biologists, especially Wegener (1915), met outraged scorn from geologists and geographers when they argued that it must have been the continents that had moved rather than the organisms that had dispersed. Eventually, however, measurements of the directions of the Earth's magnetic fields required the same, apparently wildly improbable, explanation and the critics capitulated. The discovery that the tectonic plates of the Earth's crust move and carry the migrating continents with them reconciles geologist and biologist (Figure 2.19). While major evolutionary developments were occurring in the plant and animal kingdoms, their populations were being split and separated, and land areas were moving across climatic zones. This was happening while changes in temperature were occurring on a vastly greater scale than the glacial cycles of the Pleistocene episode.

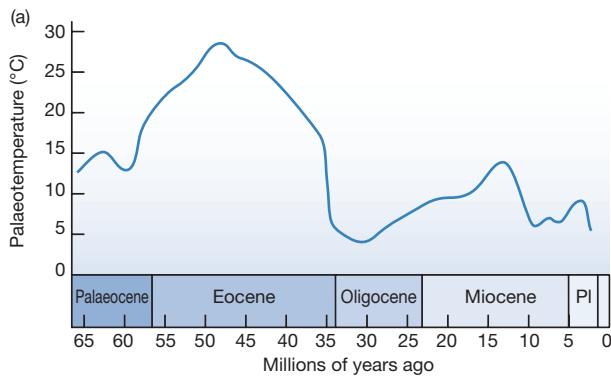
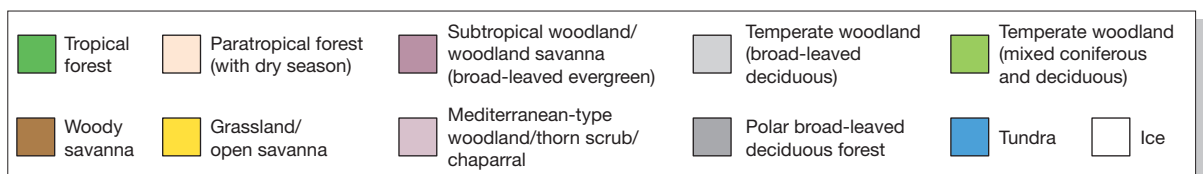
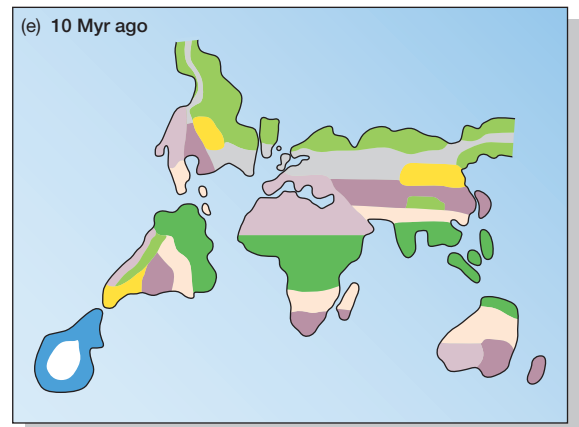
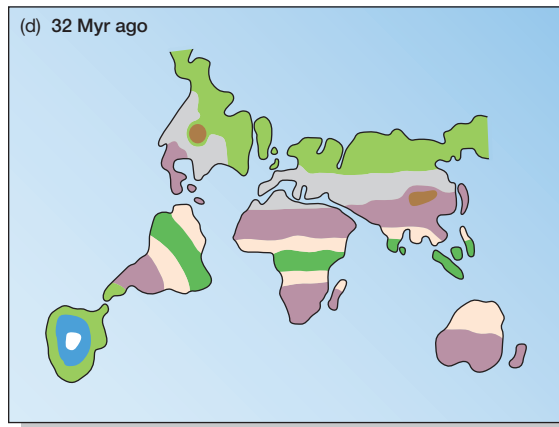
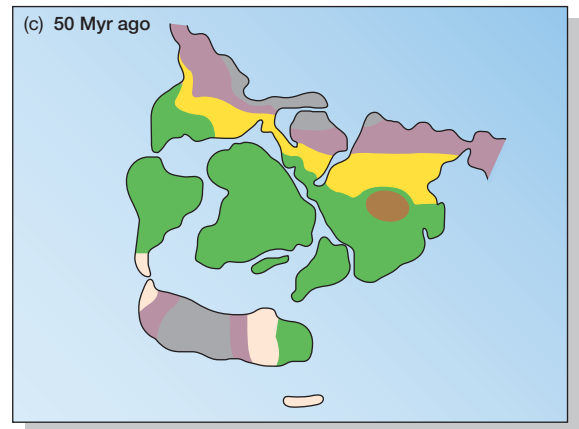
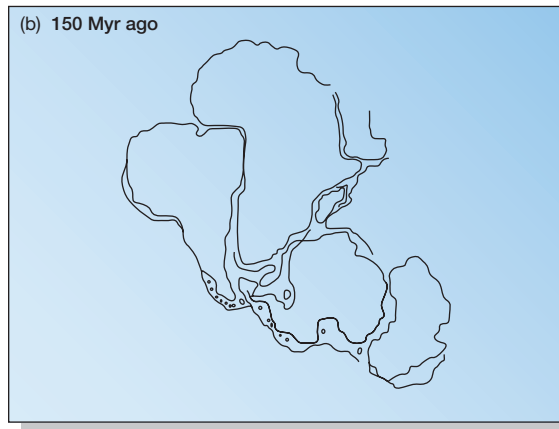


Figure 2.19

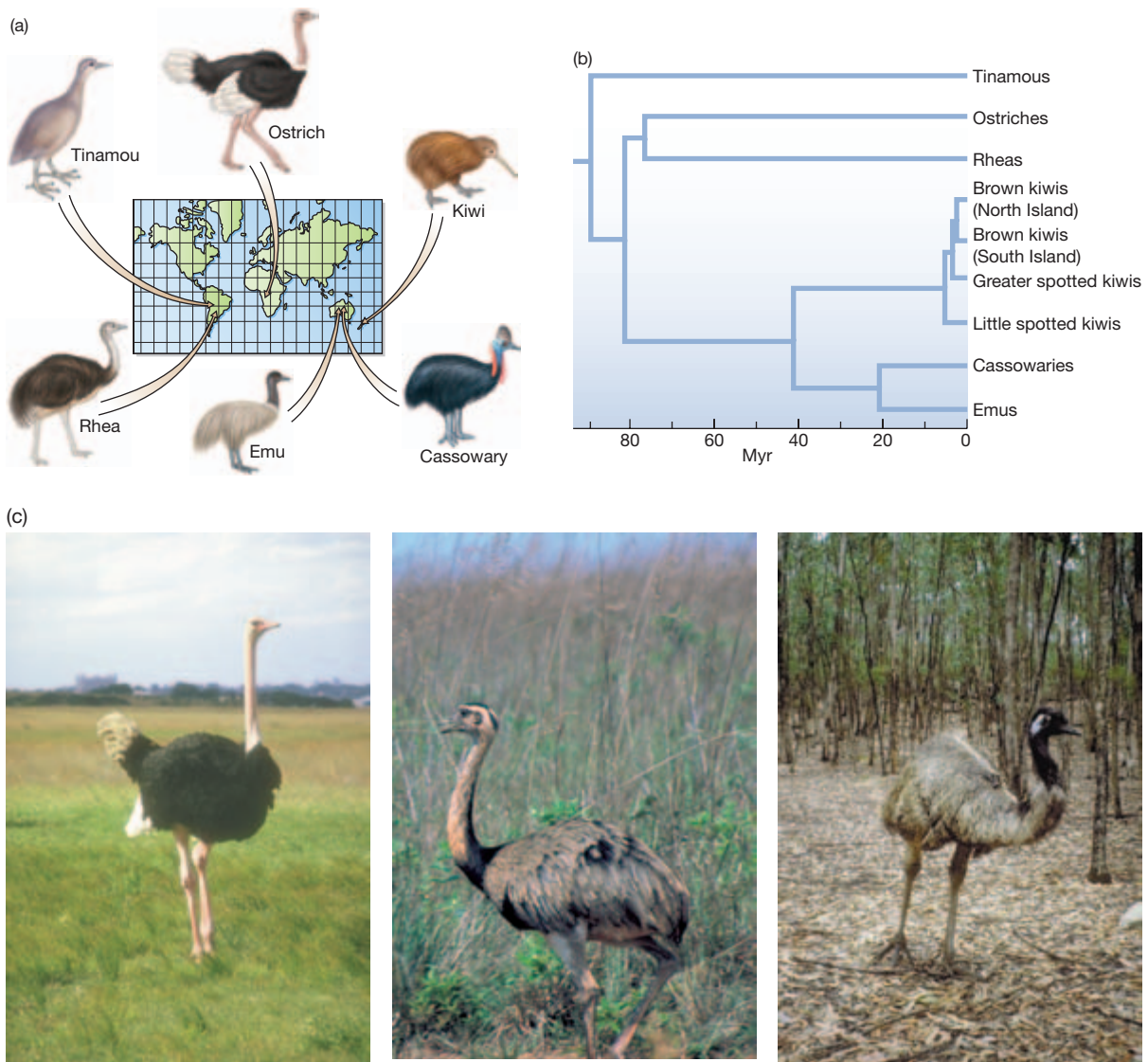
(a) Changes in temperature in the North Sea over the past 65 million years. During this period there were large changes in sea level that allowed dispersal of both plants and animals between land masses. (b–e) Continental drift. (b) The ancient supercontinent of Gondwanaland began to break up about 150 million years (Myr) ago. (c) About 50 Myr ago (early Middle Eocene) recognizable bands of distinctive vegetation had developed, and (d) by 32 Myr ago (early Oligocene) these had become more sharply defined. (e) By 10 Myr ago (early Miocene) much of the present geography of the continents had become established but with dramatically different climates and vegetation from today: the position of the Antarctic ice cap is highly schematic.





... and divided populations that have then evolved independently

The established drift of the continents answers many questions in the ecology of evolution. The curious world distribution of large flightless birds is one example (Figure 2.20a). The presence of the ostrich in Africa, the emu in Australia, and the very similar rhea in South America could scarcely be explained by dispersal



(b) AFTER DIAMOND, 1983; FROM DATA OF SIBLEY & AHLQUIST; (c) LEFT, MIDDLE) © WALT ANDERSON, VISUALS UNLIMITED

**Figure 2.20**

(a) The distribution of terrestrial flightless birds. (b) The phylogenetic tree of the flightless birds and the estimated times (million years, Myr) of their divergence. (c) Photos of large flightless birds found in three major continents: (left) the ostrich (*Struthio camelus*) is African and commonly occurs together with herds of zebra and antelope in savanna or steppe grasslands; (middle) the rhea (*Rhea americana*) is found in similar grasslands in South America (e.g. Brazil, Argentina), commonly together with herds of deer and guanacos; and (right) the emu (*Dromaius novaehollandiae*) inhabits equivalent habitats in Australia. Many other species of these very large, mainly herbivorous birds have been sought after by humans for food and have become extinct. The presence of these evolutionarily related and ecologically similar species in three widely separated continents is explained by the drifting apart of the continents from the time (150 Myr ago) when they were portions of the primitive continent of Gondwanaland (Figure 2.19).

of some common flightless ancestor. Now, techniques of molecular biology make it possible to analyze the time at which the various flightless birds started their evolutionary divergence (Figure 2.20b). The tinamous seem to have been the first to diverge and became evolutionarily separate from the rest, the *ratites*. Australasia next became separated from the other southern continents, and, from the latter, the ancestral stocks of ostriches and rheas were subsequently separated when the Atlantic opened up between Africa and South America. Back in Australasia, the Tasman Sea opened up about 80 million years ago and ancestors of the kiwi were thought to have made their way, by island hopping, about 40 million years ago across to New Zealand, where divergence into the present species happened relatively recently. The unraveling of this particular example implies the early evolution of the property of flightlessness and only subsequently the isolation of the different types between the emerging continents.

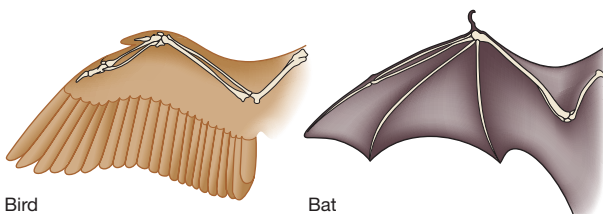
## 2.7 Interpreting the results of evolution: convergents and parallels

Flightlessness did not evolve independently on the different continents. However, there are many examples of organisms that have evolved in isolation from each other and then converged on remarkably similar forms or behavior. Such similarity is particularly striking when similar roles are played by structures that have quite different evolutionary origins – that is, when the structures are *analogous* (similar in superficial form or function) but not *homologous* (derived from an equivalent structure in a common ancestry). When this occurs, it is termed *convergent evolution*. Bird and bat wings are a classic example (Figure 2.21).

Further examples show *parallels* in the evolutionary pathways of ancestrally related groups occurring after they were isolated from each other. The classic example is provided by placental and marsupial mammals. Marsupials arrived on what would become the Australian continent in the Cretaceous period (around 90 million years ago; see Figure 2.19), when the only other mammals present were the curious egg-laying monotremes (now represented only by the spiny anteaters and the duck-billed platypus). An evolutionary process of radiation then occurred among the Australian marsupials that in many ways accurately paralleled what was occurring among the placental mammals on other continents (Figure 2.22). It is hard to escape the view that the environments of placentals and marsupials contained ecological pigeonholes (niches) into which the evolutionary process has neatly ‘fitted’ ecological equivalents. In contrast to convergent evolution, however, the marsupials and placentals started to diversify from a common ancestral line, and both inherited a common set of potentials and constraints.

convergent evolution

parallel evolution



**Figure 2.21**

Convergent evolution: the wings of bats and birds are analogous (not homologous). They are structurally different: the bird wing is supported by digit number 2 and covered with feathers; the bat wing is supported by digits 2–5 and covered with skin.



**Figure 2.22**

Parallel evolution of marsupial and placental mammals. The pairs of species are similar in both appearance and habit and usually (but not always) in lifestyle.

Doglike  
carnivore



Wolf (*Canis*)



Tasmanian wolf (*Thylacinus*)

Catlike  
carnivore



Ocelot (*Felis*)



Native cat (*Dasyurus*)

Arboreal  
glider



Flying squirrel (*Glaucomys*)



Flying phalanger (*Petaurus*)

Fossorial  
herbivore



Ground hog (*Marmota*)



Wombat (*Vombatus*)

Digging  
ant feeder



Anteater (*Myrmecophaga*)



Anteater (*Myrmecobius*)

Subterranean  
insectivore



Common mole (*Talpa*)



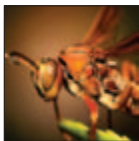
Marsupial mole (*Notoryctes*)

interpreting the match between  
organisms and their environment

When we marvel at the diversity of complex specializations by which organisms match their varied environments there is a temptation to regard each case as an example of evolved perfection. But there is nothing in the process of evolution by natural selection that implies perfection. The evolutionary process works on the genetic variation that is available. It favors only those forms that are fittest from among the range of variety available, and this may be a very restricted choice. The very essence of natural selection is that organisms come to match their environments by being ‘the fittest available’ or ‘the fittest yet’: they are not ‘the best imaginable’.

It is particularly important to realize that past events on Earth can have profound repercussions on the present. Our world has not been constructed by taking each organism in turn, testing it against each environment, and moulding it so that every organism finds its perfect place. It is a world in which organisms live where they do for reasons that are often, at least in part, accidents of history. Moreover the ancestors of the organisms that we see around us lived in environments that were profoundly different from those of the present. Evolving organisms are not free agents – some of the features acquired by their ancestors hang like millstones around their necks, limiting and constraining where they can now live and what they might become. It is very easy to wonder and marvel at how beautifully the properties of fish fit them to live in water – but just as important to emphasize that these same properties prevent them from living on land.

Having sketched out the evolutionary background for the whole of ecology in this chapter, we will return to some particular topics in evolutionary ecology in Chapter 8, especially aspects of coevolution, where interacting pairs of species play central roles in one another's evolution. However, since evolution does provide a backdrop to all ecological acts, its influence can of course be seen throughout the remainder of this book.



## Summary

### The force of natural selection

Life is represented on Earth by a diversity of specialist species, each of which is absent from almost everywhere. Early interest in this diversity mainly existed among explorers and collectors, and the idea that the diversity had arisen by evolution from earlier ancestors over geological time was not seriously discussed until the first half of the 19th century. Charles Darwin and Alfred Russel Wallace (strongly influenced by having read Malthus's essay *An Essay on the Principle of Population*) independently proposed that natural selection constituted a force that would drive a process of evolution. The theory of natural selection is an ecological theory. The reproductive potential of living organisms leads them inescapably to compete for limited resources. Success in this competition is measured by leaving more descendants than others to subsequent generations. When these ancestors differ in properties that are heritable the character of populations will necessarily change over time and evolution will happen.

Darwin had seen the power of human selection to change the character of domestic animals and plants and he recognized the parallel in natural selection. But there is one big difference: humans select for what they want in the future, but natural selection is a result of events in the past – it has no intentions and no aim.

### Natural selection in action

We can see natural selection in action within species in the variation within species over their geographic range and even over very short distances where we can detect powerful selective forces in action and recognize ecologically specialized races within species. Transplanting plants and animals between habitats reveals tightly specialized matches between organisms and their environments. The evolutionary responses of animals and plants to pollution demonstrate the speed of evolutionary change, as do experiments on the effects of predators on the evolution of their prey.

### The origin of species

Natural selection does not normally lead to the origin of species unless it is coupled with the reproductive isolation of populations from each other – as occurs for example on islands and is illustrated by the finches of the Galapagos Islands. *Biospecies* are recognized when they have diverged enough to prevent them from forming fertile hybrids if and when they meet.

### Climatic change and continental drift

Much of what we see in the present distribution of organisms is not so much a precise, locally evolved match to present environments as a fingerprint left by the hand of history. Changes in climate, particularly during the ice ages of the Pleistocene, bear a lot of the

responsibility for the present patterns of distribution of plants and animals. On a longer time scale, many distributions make sense only once we realize that while major evolutionary developments were occurring, populations were being split and separated, and land areas were moving across climatic zones.

### Parallel and convergent evolution

Evidence of the power of ecological forces to shape the direction of evolution comes from parallel evolution (in which populations long isolated from common ancestors have followed similar patterns of diversification) and from convergent evolution (in which populations evolving from very different ancestors have converged on very similar forms and behavior).

## Review questions

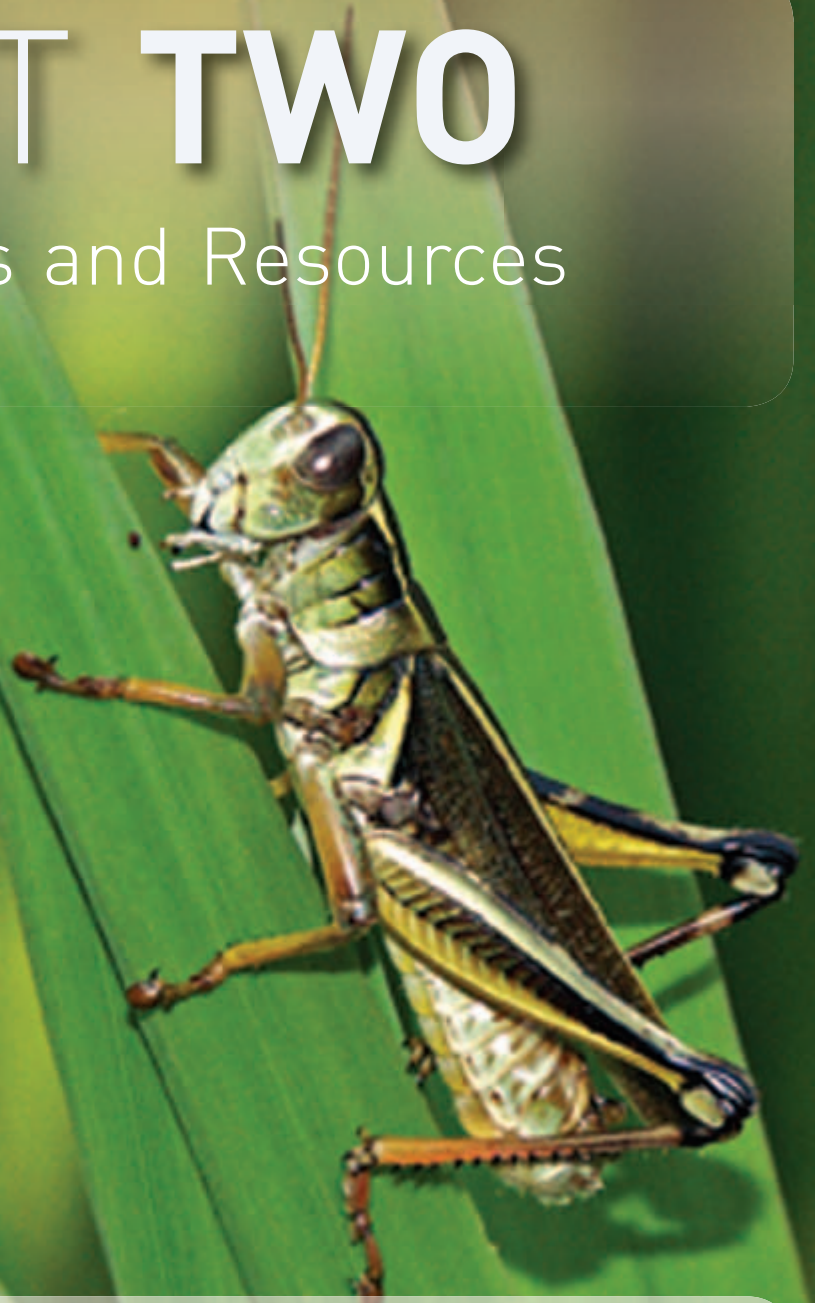
### REVIEW QUESTIONS

Asterisks indicate challenge question

- 1\* What do you consider to be the essential distinction between natural selection and evolution?
- 2 What was the contribution of Malthus to Darwin's and Wallace's ideas about evolution?
- 3 Why is 'the survival of the fittest' an unsatisfactory description of natural selection?
- 4 What is the essential difference between natural selection and the selection practiced by plant and animal breeders?
- 5 What are reciprocal transplants? Why are they so useful in ecological studies?
- 6 Is sexual selection, as practiced by guppies, different from or just part of natural selection?
- 7\* Review the utility and applicability of the biospecies concept to a range of groups, including a common species of plant, a rare animal species of conservation interest and bacteria living in the soil.
- 8 What is it about the Galapagos finches that has made them such ideal material for the study of evolution?
- 9 What is the difference between convergent and parallel evolution?
- 10\* The process of evolution can be interpreted as optimizing the fit between organisms and their environment or as narrowing and constraining what they can do. Discuss whether there is a conflict between these interpretations.

# PART TWO

## Conditions and Resources



- 3** | Physical conditions and the availability of resources 69
- 4** | Conditions, resources and the world's communities 110





# Chapter 3



## Physical conditions and the availability of resources

### *Chapter contents*

#### CHAPTER CONTENTS

- 3.1 Introduction
- 3.2 Environmental conditions
- 3.3 Plant resources
- 3.4 Animals and their resources
- 3.5 Effects of intraspecific competition for resources
- 3.6 Conditions, resources and the ecological niche

### *Key concepts*

#### KEY CONCEPTS

In this chapter you will:

- understand the nature of, and contrasts between, conditions and resources
- understand how organisms respond to the whole range of conditions like temperature, but also to 'extreme' conditions and to the timing of both variations and extremes
- appreciate how a plant's responses to, and its consumption of, the resources of solar radiation, water, minerals and carbon dioxide are intertwined
- appreciate the importance of contrasting body compositions in the consumption of plants by animals, and of overcoming defenses in the consumption of animals by other animals
- understand the effects of intraspecific competition for resources
- appreciate how responses to conditions and resources interact to determine ecological niches

*For ecologists, organisms are really only worth studying where they are able to live. The most fundamental prerequisites for life in any environment are that the organisms can tolerate the local conditions and that their essential resources are being provided. We cannot expect to go very far in understanding the ecology of any species without understanding its interactions with conditions and resources.*

### 3.1 Introduction

Conditions and resources are two quite distinct properties of environments that determine where organisms can live. Conditions are physicochemical features of the environment such as its temperature, humidity or, in aquatic environments, pH. An organism always alters the conditions in its immediate environment – sometimes on a very large scale (a tree, for example, maintains a zone of higher humidity on the ground beneath its canopy) and sometimes only on a microscopic scale (an algal cell in a pond alters the pH in the shell of water that surrounds it). But conditions are not consumed nor used up by the activities of organisms.

resources, unlike conditions,  
are consumed

Environmental resources, by contrast, *are* consumed by organisms in the course of their growth and reproduction. Green plants photosynthesize and obtain both energy and biomass from inorganic materials. Their resources are solar radiation, carbon dioxide, water and mineral nutrients. ‘Chemosynthetic’ organisms like many of the primitive Archaeobacteria obtain energy by oxidizing methane, ammonium ions, hydrogen sulfide or ferrous iron; they live in environments like hot springs and deep sea vents using resources that were abundant during early phases of life on Earth. All other organisms use the bodies of other organisms as their food. In each case, what has been consumed is no longer available to another consumer. The rabbit eaten by an eagle is not available to another eagle. The quantum of solar radiation absorbed and photosynthesized by a leaf is not available to another leaf. This has an important consequence: organisms may *compete* with each other to capture a share of a limited resource.

In this chapter we consider, first, examples of the ways in which environmental conditions limit the behavior and distribution of organisms. We draw most of our examples from the effects of temperature, which serve to illustrate many general effects of environmental conditions. We consider next the resources used by photosynthetic green plants, and then we go on to examine the ways in which organisms that are themselves resources have to be captured, grazed or even inhabited before they are consumed. Finally we consider the ways in which organisms of the same species may compete with each other for limited resources.





Penguins do not find the Antarctic in the least bit 'extreme'.

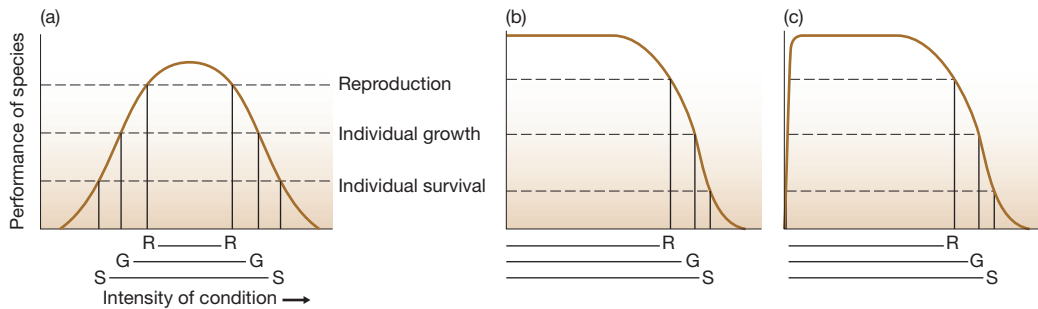
## 3.2 Environmental conditions

### 3.2.1 What do we mean by 'harsh', 'benign' and 'extreme'?

It seems quite natural to describe environmental conditions as 'extreme', 'harsh', 'benign' or 'stressful'. But these describe how we, human beings, feel about them. It may seem obvious when conditions are extreme: the midday heat of a desert, the cold of an Antarctic winter, the salt concentration of the Great Salt Lake. What this means, however, is only that these conditions are extreme *for us*, given our particular physiological characteristics and tolerances. But to a cactus there is nothing extreme about the desert conditions in which cacti have evolved; nor are the icy fastnesses of Antarctica an extreme environment for penguins. But a tropical rain forest *would* be a harsh environment for a penguin, though it is benign for a macaw; and a lake is a harsh environment for a cactus, though it is benign for a water hyacinth. There is, then, a relativity in the ways organisms respond to conditions; it is too easy and dangerous for the ecologist to assume that all other organisms sense the environment in the way we do. Emotive words like harsh and benign, even relativities such as hot and cold, should be used by ecologists only with care.

### 3.2.2 Effects of conditions

Temperature, relative humidity and other physicochemical conditions induce a range of physiological responses in organisms, which determine whether the physical environment is habitable or not. There are three basic types of *response curve* (Figure 3.1). In the first (Figure 3.1a), extreme conditions are lethal, but between the two extremes there is a continuum of more favorable conditions. Organisms are typically able to survive over the whole continuum, but can grow actively only over a more restricted range and can reproduce only within an even narrower band. This is a typical response curve for the effects of temperature or pH. In the second (Figure 3.1b), the condition is lethal only at high intensities. This is the case for poisons. At low or even zero concentration



**Figure 3.1**

Response curves illustrating the effects of a range of environmental conditions on individual survival (S), growth (G), and reproduction (R).

(a) Extreme conditions are lethal, less extreme conditions prevent growth, and only optimal conditions allow reproduction. (b) The condition is lethal only at high intensities; the reproduction–growth–survival sequence still applies. (c) Similar to (b), but the condition is required by organisms, as a resource, at low concentrations.

the organism is typically unaffected, but there is a threshold above which performance decreases rapidly: first reproduction, then growth, and finally survival. The third (Figure 3.1c), then, applies to conditions that are required by organisms at low concentrations but become toxic at high concentrations. This is the case for some minerals, such as copper and sodium chloride, that are essential resources for growth when they are present in trace amounts but become toxic conditions at higher concentrations.

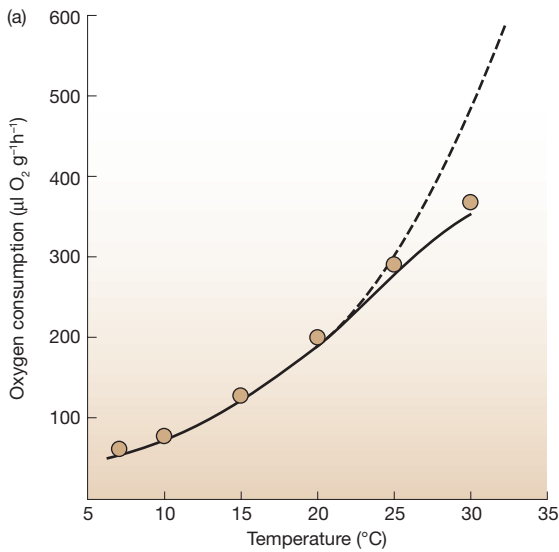
Of these three responses, the first is the most fundamental. It is accounted for, in part, by changes in metabolic effectiveness. For each 10°C rise in temperature, for example, the rate of biological processes often roughly doubles, and thus appears as an exponential curve on a plot of rate against temperature (Figure 3.2a). The increase is brought about because high temperature increases the speed of molecular movement and speeds up chemical reactions. For an ecologist, however, effects on individual chemical reactions are likely to be less important than effects on rates of growth or development or on final body size, since these tend to drive the core ecological activities of survival, reproduction and movement (see Chapter 5). And when we plot rates of growth and development of whole organisms against temperature, there is quite commonly an extended range over which there are, at most, only slight deviations from linearity (Figure 3.2b, c). Either way, at lower temperatures (though ‘lower’ varies from species to species, as explained earlier) performance is likely to be impaired simply as a result of metabolic inactivity.

Together, rates of growth and development determine the final size of an organism. For instance, for a given rate of growth, a faster rate of development will lead to smaller final size. Hence, if the responses of growth and development to variations in temperature are not the same, temperature will also affect final size. In fact, development usually increases more rapidly with temperature than does growth, such that, for a very wide range of organisms, final size tends to decrease with rearing temperature (Figure 3.3).

These effects of temperature on growth, development and size may be of practical rather than simply scientific importance. Increasingly, ecologists are called upon to predict. We may wish to know what the consequences would be, say, of a 2°C rise in temperature resulting from global warming. We cannot afford to assume

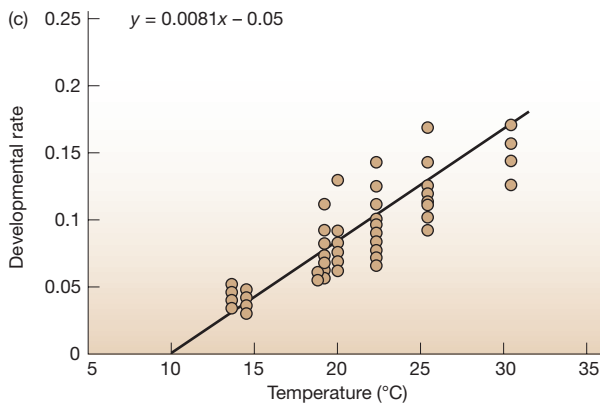
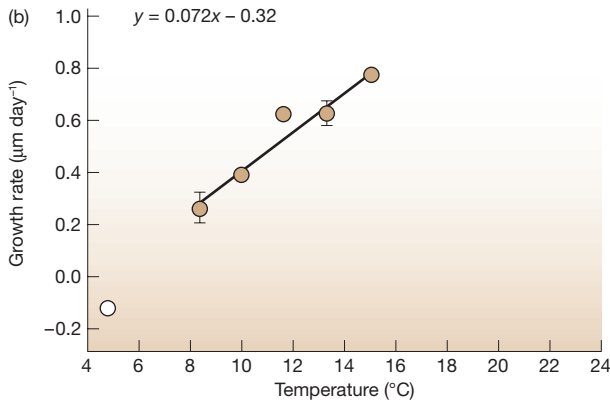
effectively linear effects of temperature on rates of growth and development

temperature and final size



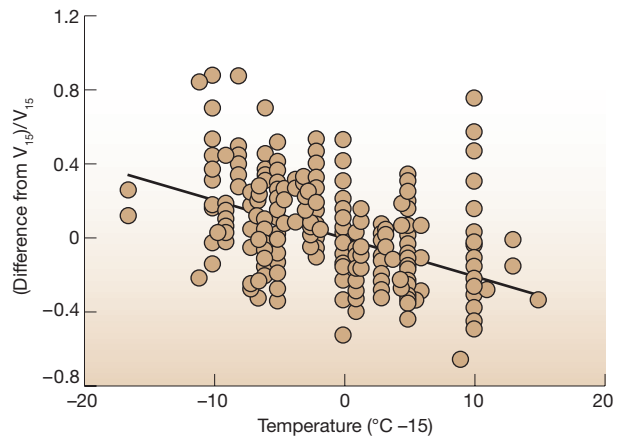
**Figure 3.2**

(a) The rate of oxygen consumption of the Colorado beetle (*Leptinotarsa decemlineata*), which increases non-linearly with temperature. It doubles for every 10°C rise in temperature up to 20°C but increases less fast at higher temperatures. (b, c) Effectively linear relationships between rates of growth and development and temperature. The linear regression equations are shown. Both are highly significant. (b) Growth of the protist *Strombidinopsis multiauris*. (c) Egg-to-adult development in the mite *Amblyseius californicus*, where the vertical scale represents the proportion of total development achieved in 1 day at the temperature concerned.



**Figure 3.3**

Final organism size decreases with increasing temperature, as illustrated in protists, single-celled organisms. Because the 72 data sets combined here were derived from studies carried out at a range of temperatures, both scales are 'standardized'. The horizontal scale measures temperature as a deviation from 15°C. The vertical scale measures size (cell volume,  $V$ ) relative to the size at 15°C. The slope of the regression line is  $-0.025$  (SE, 0.004;  $P < 0.01$ ): cell volume decreased by 2.5% for every 1°C rise in rearing temperature.



AFTER ATKINSON ET AL., 2003

high and low temperatures

exponential relationships with temperature if they are really linear, or to ignore the effects of changes in organism size on their role in ecological communities.

At extremely high temperatures, enzymes and other proteins become unstable and break down, and the organism dies. But difficulties may set in before these extremes are reached. At high temperatures, terrestrial organisms are cooled by the evaporation of water (from open stomata on the surfaces of leaves, or through sweating), but this may lead to serious, perhaps lethal, problems of dehydration; or, as water reserves run low, body temperature may rise rapidly. Even where loss of water is not a problem, for example among aquatic organisms, death is usually inevitable if temperatures are maintained for long above 60°C. The exceptions, *thermophiles*, are mostly specialized fungi and the primitive Archaeobacteria. One of these, *Pyrodicticum occultum*, can live at 105°C – something that is only possible because, under the pressure of the deep ocean, water does not boil at that temperature.

At temperatures a few degrees above zero, organisms may be forced into extended periods of inactivity and the cell membranes of sensitive species may begin to break down. This is known as *chilling injury*, which affects many tropical fruits. On the other hand, many species of both plants and animals can tolerate temperatures well below zero provided that ice does not form. If it is not disturbed, water can supercool to temperatures as low as -40°C without forming ice; but a sudden shock allows ice to form quite suddenly within plant cells, and this, rather than the low temperature itself, is then lethal, since ice formed within a cell is likely simply to disrupt and destroy it. If, however, temperatures fall slowly, ice can form between cells and draw water from within them. With dehydrated cells, the effects on plants are then very much like those of high-temperature drought.

the timing of extremes

The absolute temperature that an organism experiences is important. But the timing and duration of temperature extremes may be equally important. For example, unusually hot days in early spring may interfere with fish spawning or kill the fry but otherwise leave the adults unaffected. Similarly, a late spring frost might kill seedlings but leave saplings and larger trees unaffected. The duration and frequency of extreme conditions are also often critical. In many cases, a periodic drought or tropical storm may have a greater effect on a species' distribution than the average level of a condition. To take just one example: the saguaro cactus is



Saguaro cactus can only survive short periods at freezing temperatures.

liable to be killed when temperatures remain below freezing for 36 hours, but if there is a daily thaw it is under no threat. In Arizona, the northern and eastern edges of the cactus's distribution correspond to a line joining places where on occasional days it fails to thaw. Thus the saguaro is absent where there are occasionally lethal conditions – an individual need only be killed once.

### 3.2.3 Conditions as stimuli

Environmental conditions act primarily to modulate the rates of physiological processes. In addition, though, many conditions are important stimuli for growth and development and prepare an organism for conditions that are to come.

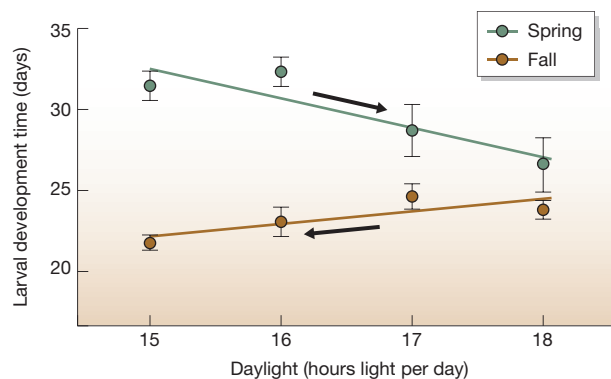
The idea that animals and plants in nature can anticipate, and be used by us to predict, future conditions ('a big crop of berries means a harsh winter to come') is the stuff of folklore. But there are important advantages to an organism that can predict and prepare for repeated events such as the seasons. For this, the organism needs an internal clock that can be used to check against an external signal. The most widely used external signal is the length of day – the photoperiod. On the approach of winter – as the photoperiod shortens – bears, cats and many other mammals develop a thickened fur coat, birds such as ptarmigan put on winter plumage, and very many insects enter a dormant phase (*diapause*) within the normal activity of their life cycle. Insects may even speed up their development as daylength decreases in the fall (as harsh winter conditions approach), but then speed up development again in the spring as daylength increases, once the pressure is on to have reached the adult stage by the start of the breeding season (Figure 3.4). Other photoperiodically timed events are the seasonal onset of reproductive activity in animals, the onset of flowering and seasonal migration in birds.

An experience of chilling is needed by many seeds before they will break dormancy. This prevents them from germinating during the moist warm weather

photoperiod is commonly used to time dormancy, flowering or migration

**Figure 3.4**

The effect of daylength on larval development time in the butterfly *Lasiommata maera* in the fall (third larval stage, before diapause) and spring. The arrows indicate the normal passage of time: daylength decreases through the fall (and development speeds up) but increases in the spring (development again speeds up). The bars are standard errors.



AFTER GOTTHARD ET AL., 1999

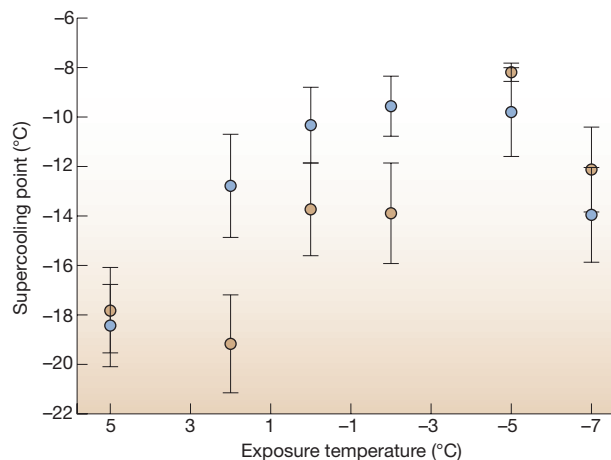
immediately after ripening and then being killed by the winter cold. As an example, temperature and photoperiod interact to control the seed germination of birch (*Betula pubescens*). Seeds that have not been chilled need an increasing photoperiod (indicative of spring) before they will germinate; but if the seed has been chilled, it starts growth without the light stimulus. Either way, growth should be stimulated only once winter has passed. The seeds of lodgepole pine, on the other hand, remain protected in their cones until they are heated by forest fire. This stimulus is an indicator that the ground has been cleared and that new seedlings have a chance of becoming established.

#### acclimatization

Conditions may themselves trigger an altered response to the same or even more extreme conditions: for instance, exposure to relatively low temperatures may lead to an increased rate of metabolism at such temperatures and/or to an increased tolerance of even lower temperatures. This is the process of *acclimatization* (called *acclimation* when induced in the laboratory). Antarctic springtails (tiny arthropods), for instance, when taken from ‘summer’ temperatures in the field (around 5°C in the Antarctic) and subjected to a range of acclimation temperatures, responded to temperatures in the range +2°C to -2°C (indicative of winter) by showing a marked drop in the temperature at which they froze (Figure 3.5); but at lower acclimation temperatures still (-5°C, -7°C), they

**Figure 3.5**

Acclimation to low temperatures. Samples of the Antarctic springtail *Cryptopygus antarcticus* were taken from field sites in the summer (ca. 5°C) on a number of days and their supercooling point (at which they froze) determined either immediately (controls, blue circles) or after a period of acclimation (brown circles) at the temperatures shown. The supercooling points of the controls themselves varied because of temperature variations from day to day, but acclimation at temperatures in the range +2°C to -2°C (indicative of winter) led to a drop in the supercooling point, whereas no such drop was observed at higher temperatures (indicative of summer) or lower temperatures (too low for a physiological acclimation response). Bars are standard errors.



AFTER WORLAND &amp; CONVEY, 2001

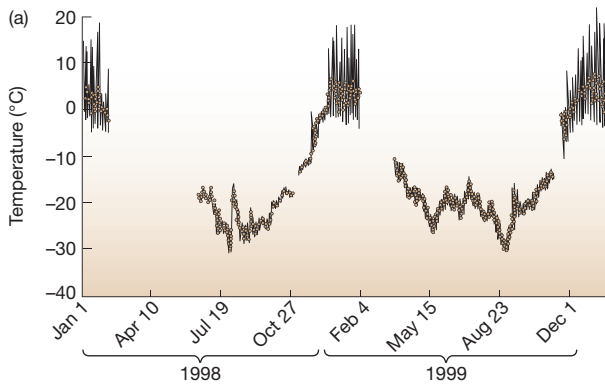
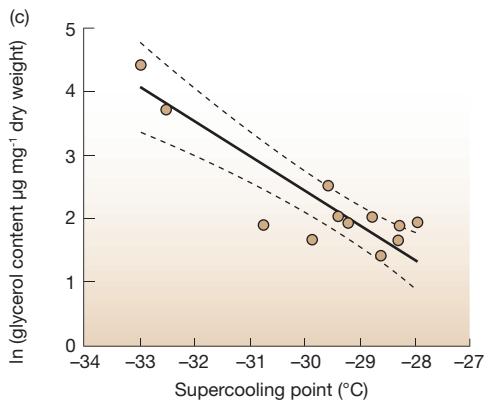
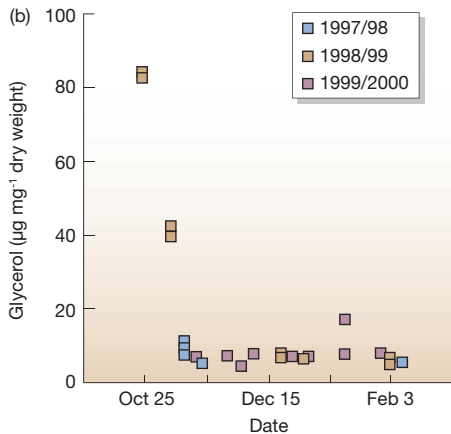


Figure 3.6

(a) Daily mean (points), maximum and minimum (tops and bottoms of lines, respectively) temperatures at Cape Bird, Ross Island, Antarctica. (b) Changes in the glycerol content of the springtail, *Gomphiocephalus hodgsoni*, from Cape Bird, which protect it from freezing (see (c)). This was extremely high over winter (as represented by the October value, the end of winter), but dropped to low values in the southern summer, when there was little need for any protection against freezing. (c) Confirmation that the supercooling point (at which ice forms) drops in the springtail as glycerol concentration increases.



AFTER SINCLAIR AND SUIRSEN, 2001

showed no such drop because the temperatures were themselves too low for the physiological processes required to make the acclimation response. One way in which such increased tolerance is achieved is by forming chemicals that act as antifreeze compounds: they prevent ice from forming within the cells and protect their membranes if ice does form (Figure 3.6). Acclimatization in some deciduous trees (frost hardening) can increase their tolerance of low temperatures by as much as 100°C.



### 3.2.4 The effects of conditions on interactions between organisms

conditions may affect the availability of a resource, . . .

Although organisms respond to each condition in their environment, the effects of conditions may be determined largely by the responses of other community members. Temperature, for example, does not act on one species alone: it also acts on its competitors, prey, parasites and so on. Most especially, an organism will suffer if its food is another species that cannot tolerate an environmental condition. This is illustrated by the distribution of the rush moth (*Coleophora alticolella*) in England. The moth lays its eggs on the flowers of the rush (*Juncus squarrosus*) and the caterpillars feed on the developing seeds. Above 600 m, the moths and caterpillars are little affected by the low temperatures, but the rush, although it grows, fails to ripen its seeds. This, in turn, limits the distribution of the moth, because caterpillars that hatch in the colder elevations will starve as a result of insufficient food (Randall, 1982).

. . . the development of disease . . .

The effects of conditions on disease may also be important. Conditions may favor the spread of infection (e.g. winds carrying fungal spores), or favor the growth of the parasite, or weaken or strengthen the defenses of the host. For example, fungal pathogens of grasshopper, *Camnula pellucida*, in the United States develop faster at warmer temperatures, but they fail to develop at all at temperatures around 38°C and higher (Figure 3.7a), and grasshoppers that regularly experience such temperatures effectively escape serious infection (Figure 3.7b), which they do by ‘basking’, allowing solar radiation to raise their body temperatures by as much as 10–15°C above the air temperature around them (Figure 3.7c).

. . . or competition

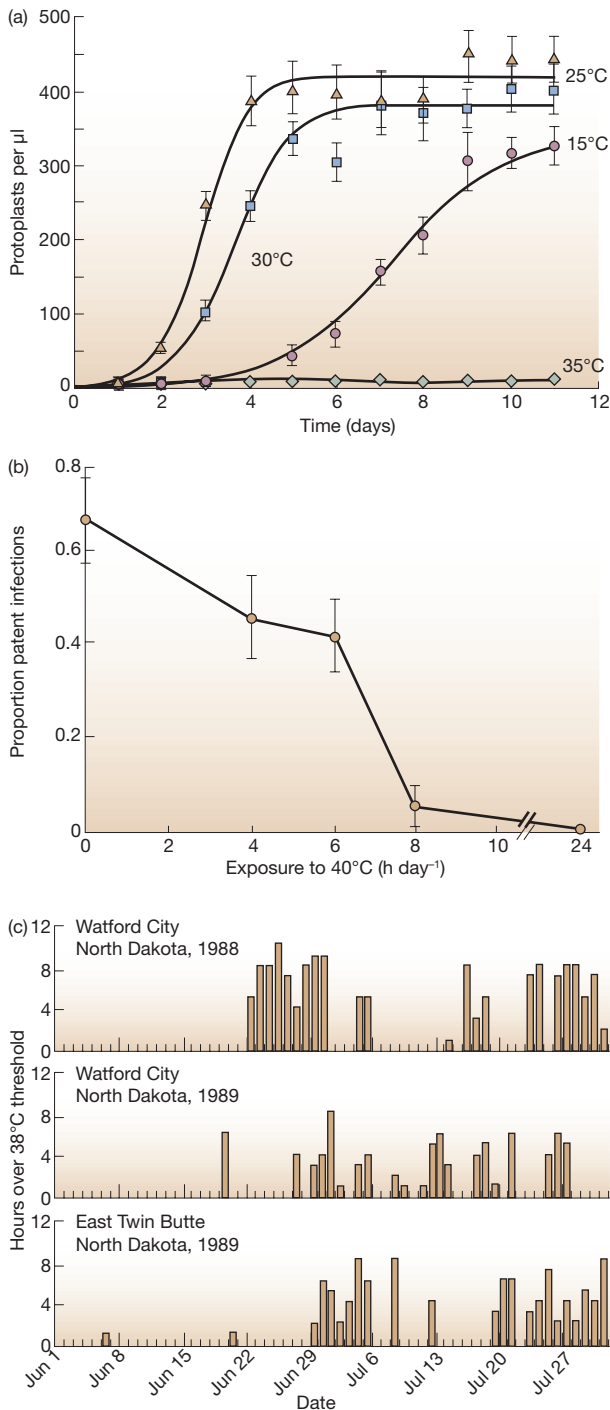
Competition between species can also be profoundly influenced by environmental conditions, especially temperature. Two stream salmonid fishes, *Salvelinus malma* and *S. leucomaenis*, coexist at intermediate altitudes (and therefore intermediate temperatures) on Hokkaido Island, Japan, but only the former lives at higher altitudes (lower temperatures) and only the latter at lower altitudes. A reversal of the outcome of competition between the species, brought about by a change in temperature, appears to play a key role in this. For example, in experimental streams supporting the two species maintained at 6°C over a 191-day period (a typical high-altitude temperature), the survival of *S. malma* was far superior to that of *S. leucomaenis*; whereas at 12°C (typical low-altitude temperature), both species survived less well, but the outcome was so far reversed that by around 90 days all of the *S. malma* had died (Figure 3.8). Both species are quite capable, alone, of living at either temperature.

### 3.2.5 Responses by sedentary organisms

Motile animals have some choice over where they live: they can show preferences. They may move into shade to escape from heat or into the sun to warm up. Such choice of environmental conditions is denied to fixed or sedentary organisms. Plants are obvious examples, but so are many aquatic invertebrates such as sponges, corals, barnacles, mussels and oysters.

form and behavior may change with the seasons

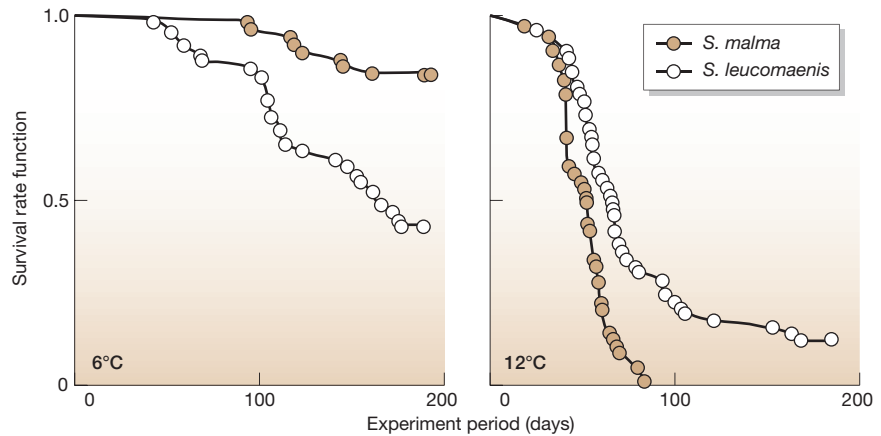
In all except equatorial environments, physical conditions follow a seasonal cycle. Indeed, there has long been a fascination with organisms’ responses to these (Box 3.1). Morphological and physiological characteristics can never be ideal for all phases in the cycle, and the jack-of-all-trades is master of none. One solution

**Figure 3.7**

The effect of temperature on the interaction between the fungal pathogen, *Entomophaga grylli*, and the grasshopper, *Camnula pellucida*. (a) Growth curves over time of the pathogen (expressed as protoplasts per  $\mu\text{l}$ ) at a range of temperatures: growth ceases at temperatures of around 38°C and higher. (b) The proportion of grasshoppers with patent (i.e. observable) infection with the pathogen drops sharply as grasshoppers spend more of their time at such higher temperatures. (c) Grasshoppers at two sites over 2 years did frequently raise their body temperatures to such high levels by basking.

**Figure 3.8**

Changing temperature reverses the outcome of competition. At low temperature (6°C) on the left, the salmonid fish *Salvelinus malma* out-survives cohabiting *S. leucomaenis*, whereas at 12°C, right, *S. leucomaenis* drives *S. malma* to extinction. Both species are quite capable, alone, of living at either temperature.



AFTER TANGUCHI & MAKINO, 2000



## 3.1 HISTORICAL LANDMARKS

### 3.1 Historical landmarks

#### Recording seasonal changes

Recording the changing behavior of organisms through the season (*phenology*) was essential before agricultural activities could be intelligently timed. The earliest phenological records were apparently the Wu Hou observations made in the Chou and Ch'in (1027–206 BC) dynasties. The date of the first flowering of cherry trees has been recorded at Kyoto, Japan, since AD 812.

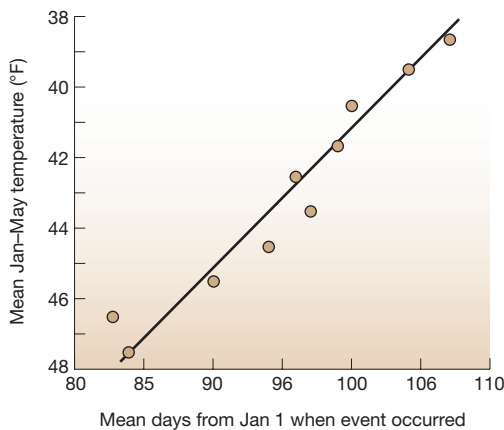
A particularly long and detailed record was started in 1736 by Robert Marsham at his estate near the city of Norwich, England. He called these records 'Indications of the spring'. Recording was continued by his descendants until 1947. Marsham recorded 27 phenological events every year: the first flowering of snowdrop, wood anemone, hawthorn and turnip; the first leaf emergence of 13 species of tree; and various animal events such as the first appearance of migrants (swallow, cuckoo, nightingale), the first nest building by rooks, croaking of frogs and toads, and the appearance of the brimstone butterfly.

Long series of measurements of environmental temperature are not available for comparison with the whole period of Marsham's records, but they are available from 1771 for Greenwich, about 160 km

away. There is surprisingly close agreement between many of the flowering and leaf emergence events at Marsham and the mean January–May temperature at Greenwich (Figure 3.9). However, not surprisingly, events such as the time of arrival of migrant birds bears little relationship to temperature.

Analysis of the Marsham data for the emergence of leaves on six species of tree indicates that the mean date of leafing is advanced by 4 days for every 1°F increase in the mean temperature from February to May (Figure 3.10). Similarly, for the eastern United States, Hopkins' *bioclimatic law* states that the indicators of spring such as leafing and flowering occur 4 days later for every 1° latitude northward, 5° longitude westward or 400 feet (c. 120 m) of altitude.

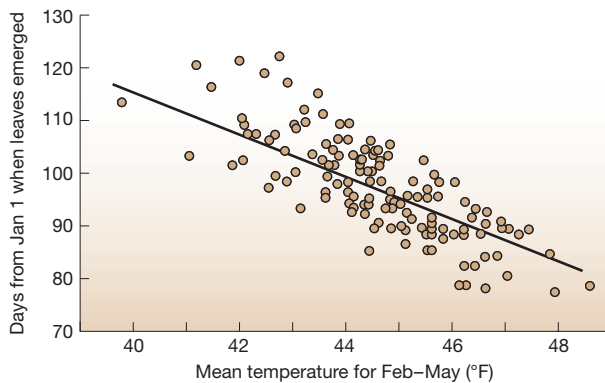
Collecting phenological records has now been transformed from the pursuit of gifted amateurs to sophisticated programs of data collection and analysis. At least 1500 phenological observation posts are now maintained in Japan alone. The vast accumulations of data have suddenly become exciting and relevant as we try to estimate the changes in floras and faunas that will be caused by global warming.



**Figure 3.9**

The relationships between mean January–May temperatures and the annual mean dates of 10 flowering and leafing events from the classic Marham records started in 1736.

FROM REDRAWN FIGURES OF MARGARY, IN FORD, 1982



**Figure 3.10**

The relationship between the mean temperature in the 4-month period, February–May, and the average date of six leafing events. The correlation coefficient is  $-0.81$ .

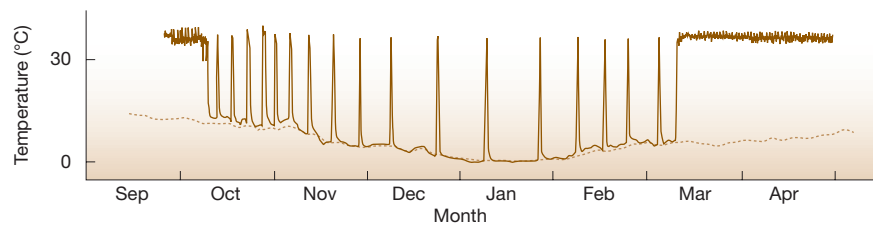
FROM REDRAWN FIGURES OF KINGTON, IN FORD, 1982

is for the morphological and physiological characteristics to keep changing with the seasons (or even anticipating them, as in acclimatization). But change may be costly: a deciduous tree may have leaves ideal for life in spring and summer but faces the cost of making new ones every year. An alternative is to economize by having long-lasting leaves like those of pines, heathers and the perennial shrubs of deserts. Here, though, there is a cost to be paid in the form of more sluggish physiological processes. Different species have evolved different compromise solutions.

### 3.2.6 Animal responses to environmental temperature

Most species of animals are, like plants, *ectotherms*: they rely on external sources of heat to determine the pace of their metabolism. This includes the invertebrates and also fish, amphibians and lizards. Others, mainly birds and mammals, are *endotherms*: they can regulate their body temperature by producing heat within their body.

ectotherms and endotherms



**Figure 3.11**

Changes in the body temperature over the 1996/97 winter of the European ground squirrel, *Spermophilus citellus* (solid line) compared to ambient soil temperature (dotted line) at the same depth at which it was hibernating. Note that during hibernation (early October to mid-March), body temperature was mostly indistinguishable from ambient temperature, apart from repeated brief periods of activity accompanied by 'normal' body temperatures.

AFTER HUT ET AL., 2002

The distinction between ectotherms and endotherms is not absolute. Some typical ectotherms, some insects for example, can control body temperature through muscle activities (e.g. shivering flight muscles). Some fish and reptiles can generate heat for limited periods of time, and even some plants can use metabolic activity to raise the temperature of their flowers. Some typical endotherms, on the other hand, such as dormice, hedgehogs and bats, allow their body temperature to fall and become scarcely different from that of their surroundings when they are hibernating (Figure 3.11).

Despite these overlaps, endothermy is inherently a different strategy from ectothermy. Over a certain narrow temperature range, an endotherm consumes energy at a basal rate. But at environmental temperatures further and further above or below that zone, endotherms expend more and more energy maintaining their constant body temperature. This makes them relatively independent of environmental conditions and allows them to stay longer at or close to peak performance. It makes them more efficient in both searching for food and escaping from predators. However, there is a cost – a high requirement for food to fuel this strategy.

The idea that organisms are harmed (and limited in their distributions) by environmental conditions not 'directly', but because of the energetic costs required to tolerate those conditions, is illustrated by a study examining the effect of a different condition: salinity. The freshwater shrimps *Palaemonetes pugio* and *P. vulgaris*, for example, co-occur in estuaries on the eastern coast of the USA at a wide range of salinities, but the former seems to be more tolerant of lower salinities than the latter, occupying some habitats from which the latter is absent. Figure 3.12 shows the mechanism likely to be underlying this. Over the low salinity range (though not at the effectively lethal lowest salinity) metabolic expenditure was significantly lower in *P. pugio*. *P. vulgaris* requires far more energy simply to maintain itself, putting it at a severe disadvantage in competition with *P. pugio*.

Endotherms have morphological modifications that reduce their energetic costs. In cold climates most have low surface area to volume ratios (short ears and limbs), and this reduces heat loss through surfaces. Typically, endotherms that live in polar environments are insulated from the cold with extremely dense fur (polar bears, mink, foxes) or feathers and extra layers of fat. In contrast, desert endotherms often have thin fur, and long ears and limbs, which help dissipate heat.

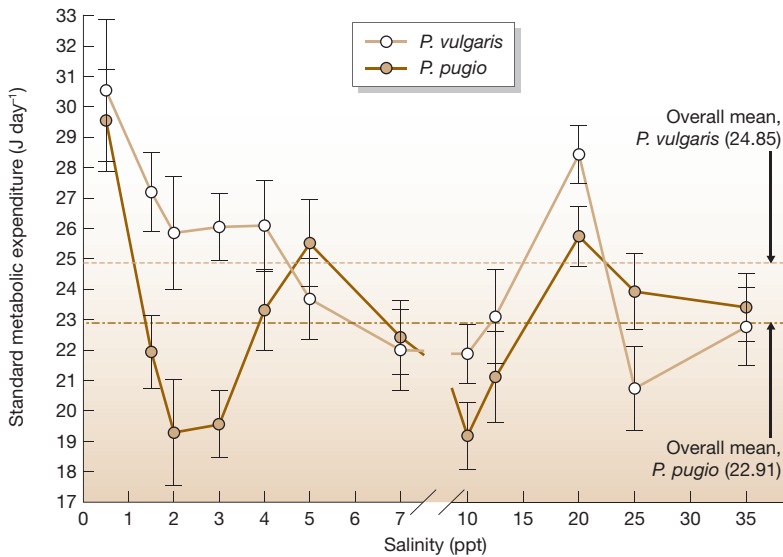


Figure 3.12

Standard metabolic expenditure (estimated through minimum oxygen consumption) in two species of shrimp, *Palaemonetes pugio* and *P. vulgaris*, at a range of salinities. There was significant mortality of both species over the experimental period at 0.5 ppt (parts per thousand), especially *P. vulgaris* (75% compared to 25%).

Variability of conditions can set biological challenges as great as extremes. Seasonal cycles, for example, can expose an animal to summer heat close to its thermal maximum, and winter chill close to its thermal minimum. Responses to these changing conditions include the laying down of different coats in the fall (thick and underlain by a thick fat layer) and in the spring (a thinner coat and loss of the dense fat layer) (Figure 3.13). Some animals also take advantage of each other's body heat as a means to cope with cold weather by huddling together. Hibernation – relaxing temperature control – allows some vertebrates to survive periods of winter cold and food shortage (see Figure 3.11) by *avoiding* the difficulties of finding sufficient fuel over these periods. Migration is another avoidance strategy: the Arctic tern, to take an extreme example, travels from the Arctic to the Antarctic and back each year, experiencing only the polar summers.

temperatures that vary seasonally pose special problems

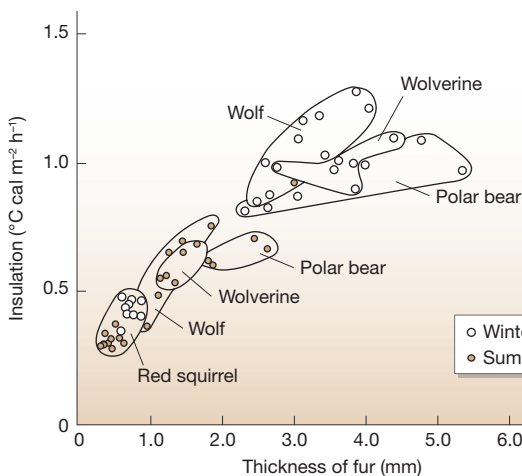


Figure 3.13

Seasonal changes in the thickness of the insulating fur coats of some Arctic and northern temperate mammals.

The thick, white winter coat and the thinner, browner summer coat of the Arctic fox.



### 3.2.7 Microorganisms in extreme environments

Microorganisms survive and grow in all the environments that are lived in or tolerated by animals and plants, and they show the same range of strategies – avoid, tolerate or specialize. Many microorganisms produce resting spores that survive drought, high temperature or cold. There are also some that are capable of growth and multiplication in conditions far outside the range of tolerance of higher organisms: they inhabit some of the most extreme environments on Earth. Temperatures maintained higher than 45°C are lethal to almost all plants and animals, but thermophilic (‘temperature loving’) microbes grow at much higher temperatures. Although similar in many ways to heat-intolerant microbes, the enzymes of these thermophiles are stabilized by especially strong ionic bonds.

Microbial communities that not only tolerate but grow at low temperatures are also known; these include photosynthetic algae, diatoms and bacteria that have been found on Antarctic sea ice. Microbial specialists have also been identified from other rare or peculiar environments: for example *acidophiles*, which thrive in environments that are highly acidic. One of them, *Thiobacillus ferrooxidans*, is found in the waste from industrial metal-leaching processes and tolerates pH 1.0. At the other end of the pH spectrum, the cyanobacterium, *Plectonema nostocorum*, from soda lakes can grow at pH 13. As noted previously, these oddities may be relicts from environments that prevailed much earlier in Earth’s history. Certainly, they warn us against being too narrow-minded when we consider the kind of organism we might look for on other planets.

## 3.3 Plant resources

Resources may be either biotic or abiotic components of the environment: they are whatever an organism uses or consumes in its growth and maintenance, leaving less available for other organisms. When a photosynthesizing leaf intercepts radiation, it deprives some of the leaves or plants beneath it. When a caterpillar eats a leaf, there is less leaf material available for other caterpillars. By their nature, resources are critical for survival, growth and reproduction and also inherently a potential source of conflict and competition between organisms.

If an organism can move about, it has the potential to search for its food. Organisms that are fixed and ‘rooted’ in position cannot search. They must rely on growing toward their resources (like a shoot or root) or catching resources that move to them. The most obvious examples are green plants, which depend

resource requirements of  
non-motile organisms



on: (i) energy that radiates to them; (ii) atmospheric carbon dioxide that diffuses to them; (iii) mineral cations that they obtain from soil colloids in exchange for hydrogen ions; and (iv) water and dissolved anions that the roots absorb from the soil. In the following sections, we concentrate on green plants. But it is important to remember that many of the non-mobile animals, like corals, sponges and bivalve mollusks, depend on resources that are suspended in the watery environment and are captured by filtering the water or even just waiting for them open-mouthed.

### 3.3.1 Solar radiation

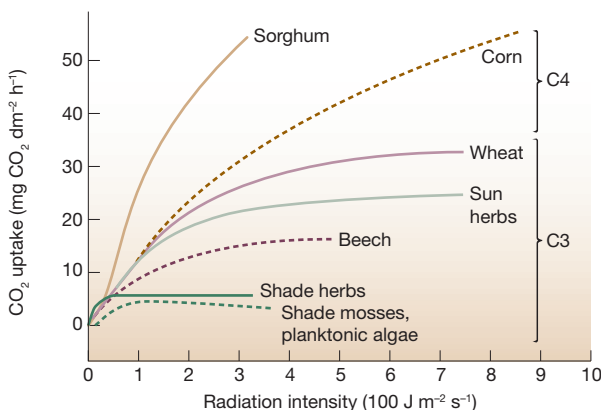
Solar radiation is a critical resource for green plants. We often refer to it loosely as 'light', but green plants actually use only about 44% of that narrow part of the spectrum of solar radiation that is visible to us between infrared and ultraviolet. The rate of photosynthesis increases with the intensity of the radiation that a leaf receives, but with diminishing returns; and this relationship itself varies greatly between species (Figure 3.14), especially between those that usually live in shaded habitats (which reach saturation at low radiation intensities) and those that normally experience full sunlight and can take advantage of it. Moreover, at high intensities, *photoinhibition* of photosynthesis may occur, such that the rate of fixation of carbon *decreases* with increasing radiation intensity. High intensities of radiation may also lead to dangerous overheating of plants. Radiation is an essential resource for plants, but they can have too much as well as too little.

The solar radiation that reaches a plant is forever changing. Its angle and intensity change in a regular and systematic way annually, diurnally and with depth within the canopy or in a water body (Figure 3.15). There are also irregular, unsystematic variations due to changes in cloud cover or shadowing by the leaves of neighboring plants. As light flecks pass over leaves lower in the canopy, they receive seconds or minutes of direct bright light and then plunge back into shade. The daily photosynthesis of a leaf integrates these various experiences; the whole plant integrates the diverse exposure of its various leaves.

There is enormous variation in the shapes and sizes of leaves. Most of the heritable variation in shape has probably evolved under selection not primarily for high photosynthesis, but rather for optimal efficiency of water use (photosynthesis achieved per unit of water transpired) and minimization of the damage done by foraging herbivores. Not all the variations in leaf shape are heritable, though:

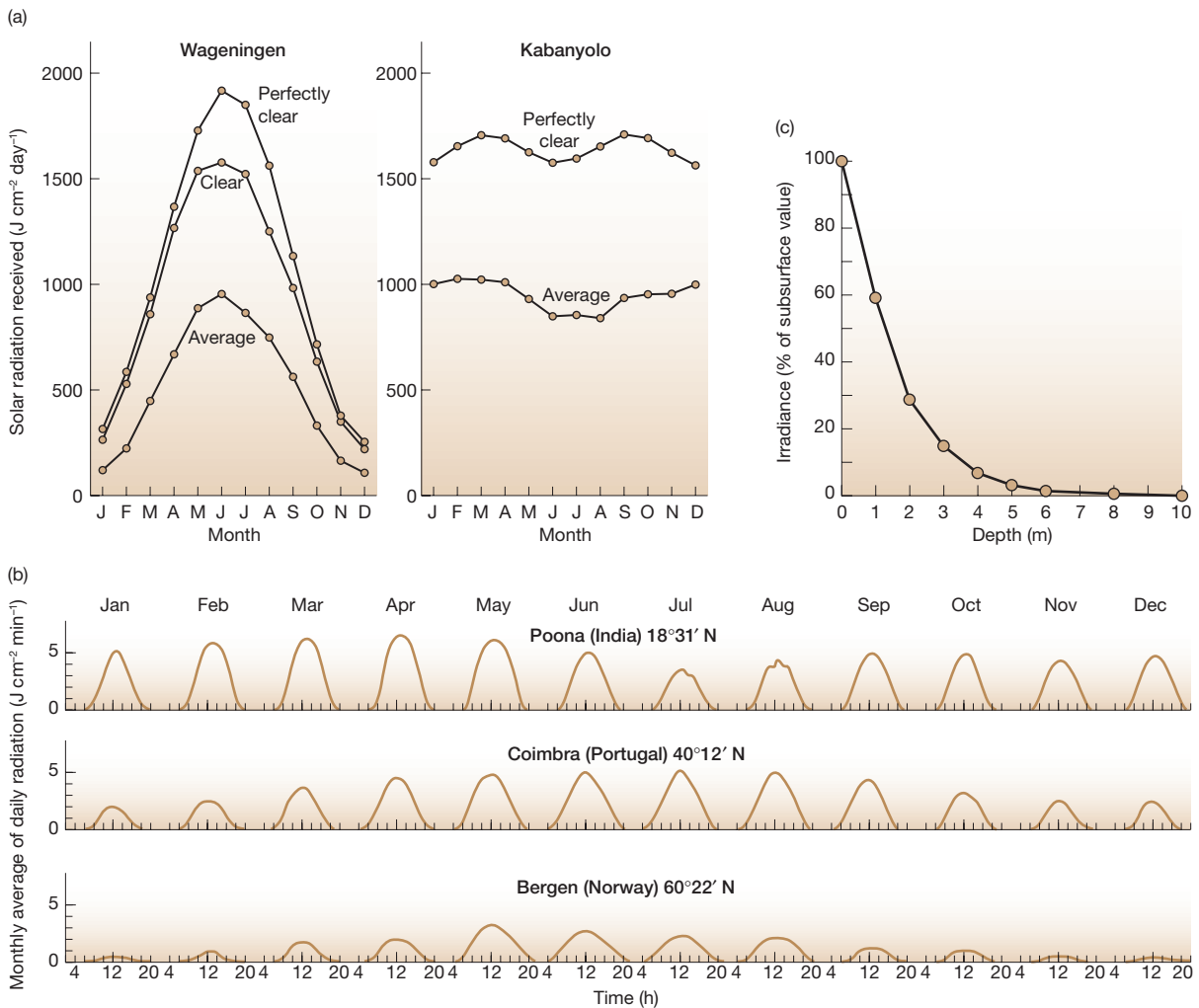
sun and shade species

sun and shade leaves



**Figure 3.14**

The response of photosynthesis by the leaves of various types of green plant (measured as carbon dioxide uptake) to the intensity of solar radiation at optimal temperatures and with a natural supply of carbon dioxide. (The different physiologies of C3 and C4 plants are explained later in Section 3.3.2.)



**Figure 3.15**

(a) The daily totals of solar radiation received throughout the year at Wageningen (the Netherlands) and Kabanyolo (Uganda). (b) The monthly average of daily radiation recorded at Poona (India), Coimbra (Portugal) and Bergen (Norway). (c) Exponential diminution of radiation intensity with water depth in a freshwater habitat (Burrinjuck Dam, Australia).

many are responses by the individual to its immediate environment. Many trees, especially, produce different types of leaf in positions exposed to full sunlight ('sun leaves') and in places lower in the canopy where they are shaded ('shade leaves'). Sun leaves are thicker, with more densely packed chloroplasts (which process the incoming radiation) within cells and more cell layers. The more flimsy shade leaves intercept diffused and filtered radiation low in the canopy but may nonetheless supplement the main photosynthetic activity of the sun leaves high in the canopy.

#### sun and shade plants

Among herbaceous plants and shrubs, specialist 'sun' or 'shade' *species* are much more common. Leaves of sun plants are commonly exposed at acute angles to the midday sun and are typically superimposed into a multilayered canopy,

where even the lower leaves may have a positive rate of net photosynthesis. The leaves of shade plants are typically arranged in a single-layered canopy and angled horizontally, maximizing their ability fully to capture the available radiation.

Other species develop as sun or shade plants, depending on where they grow. One such is the evergreen shrub, *Heteromeles arbutifolia*, which grows both in chaparral habitats in California, where shoots in the upper crown are regularly exposed to full sunlight and high temperatures, and also in shaded woodland habitats, where it receives around one-seventh as much radiation. A detailed study of this plant captures many of the points made above (Figure 3.16). As expected,

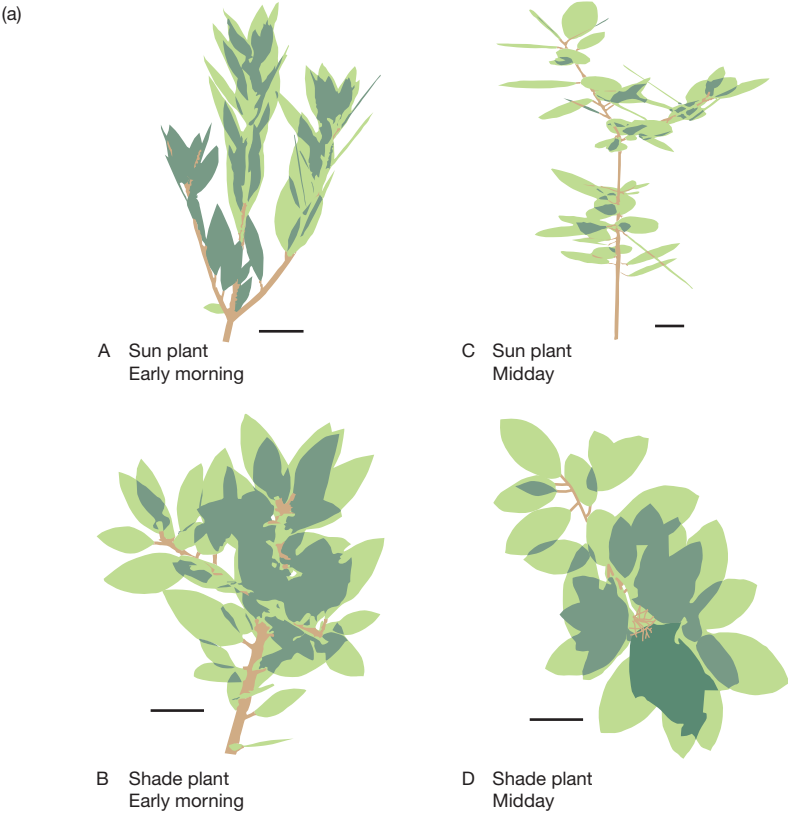


Figure 3.16

(a) Computer reconstructions of stems of typical sun (A, C) and shade (B, D) plants of the evergreen shrub *Heteromeles arbutifolia*, viewed along the path of the sun's rays in the early morning (A, B) and at midday (C, D). Darker tones represent parts of leaves shaded by other leaves of the same plant. Bars = 4 cm. (b) Observed differences in the leaves of sun and shade plants. Standard deviations are given in parentheses; the significance of differences are given following analysis of variance. (c) Consequent whole-plant properties of sun and shade plants. Letter codes indicate groups that differed significantly in analyses of variance ( $P < 0.05$ ).

(b)

	Sun		Shade		P
Leaf angle (degrees)	71.3	(16.3)	5.3	(4.3)	<0.01
Leaf blade thickness ( $\mu\text{m}$ )	462.5	(10.9)	292.4	(9.5)	<0.01
Photosynthetic capacity, area basis ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	14.1	(2.0)	9.0	(1.7)	<0.01
Chlorophyll content, area basis ( $\text{mg m}^{-2}$ )	280.5	(15.3)	226.7	(14.0)	<0.01
Leaf nitrogen content, area basis ( $\text{g m}^{-2}$ )	1.97	(0.25)	1.71	(0.21)	<0.05

(c)

	Sun plants		Shade plants	
	Summer	Winter	Summer	Winter
Fraction self-shaded	0.22 <sup>a</sup>	0.42 <sup>b</sup>	0.47 <sup>b</sup>	0.11 <sup>a</sup>
Display efficiency	0.33 <sup>a</sup>	0.38 <sup>a,b</sup>	0.41 <sup>b</sup>	0.43 <sup>b</sup>
Absorption efficiency	0.28 <sup>a</sup>	0.44 <sup>b</sup>	0.55 <sup>c</sup>	0.53 <sup>c</sup>

the leaves of sun plants are thicker and have a greater photosynthetic capacity (more chlorophyll and nitrogen) per unit leaf area than those of shade plants (Figure 3.16b). As expected, too, sun-plant leaves are inclined at a much steeper angle to the horizontal, and they therefore absorb the direct rays of the overhead summer sun over a wider leaf area than the more horizontal shade-plant leaves. The more angled leaves of sun plants, though, are also less likely than shade-plant leaves to shade other leaves of the same plant from the overhead rays of the summer sun (Figure 3.16c). But in winter, when the sun is much lower in the sky, it is the shade plants that are much less subject to this ‘self-shading’. The overall consequence of these differences is that ‘display efficiency’ – the proportion of incident radiation intercepted per unit area of leaf – is higher in shade than in sun plants, in summer because of the more horizontal leaves, but in the winter because of the relative absence of self-shading.

The properties of whole plants of *H. arbutifolia*, then, reflect both plant architecture and the morphologies and physiologies of individual leaves. The efficiency of light absorption per unit of biomass is massively greater for shade than for sun plants (Figure 3.16c), reflecting leaf angles, self-shading and leaf thickness. Overall, despite receiving only one-seventh of the radiation of sun plants, shade plants reduce the differential in their daily rate of carbon gain from photosynthesis to only a half. They successfully counterbalance their reduced photosynthetic capacity at the leaf level with enhanced light-harvesting ability at the whole-plant level. The sun plants, on the other hand, can be seen as striking a compromise between maximizing whole-plant photosynthesis while avoiding photoinhibition and overheating of individual leaves.

### 3.3.2 Water

water is lost from plants that photosynthesize

Most plant parts are largely composed of water. In some soft leaves and fruits, as much as 98% of the volume may be water. Yet this is a minute fraction of the water that passes from the soil through a plant to the atmosphere during plant growth. Photosynthesis depends on the plant absorbing carbon dioxide. This can only happen across surfaces that are wet – most notably the walls of the photosynthesizing cells in leaves. If a leaf allows carbon dioxide to enter, it is almost impossible to prevent water vapor from leaving. Likewise, any mechanism or process that slows down the rate of water loss, such as closing the stomata (pores) on the leaf surface, is almost bound to reduce the rate of carbon dioxide absorption and hence reduce the rate of photosynthesis.

wilting

Green plants serve as wicks that conduct water from the soil and release it to the atmosphere. If the rate of uptake falls below the rate of release, the body of the plant starts to dry out. The cells lose their turgidity and the plant wilts. This may just be temporary (though it may happen every day in summer), and they may recover and rehydrate at night. But if the deficit accumulates, the plant may die.

plant life in water deficit: avoiders and tolerators

Species of green plants differ in the ways in which they survive in dry environments. One strategy is to avoid the problems. *Avoiders* such as desert annuals, annual weeds and most crop plants have a short lifespan: their photosynthetic activity is concentrated during periods when they can maintain a positive water balance. For the remainder of the year, they remain dormant as seeds, a stage that requires neither photosynthesis nor transpiration. Some perennial plants shed

their photosynthetic tissues during periods of drought. Some species then replace them with new leaf forms that are less extravagant of water or spend the driest season with no leaves at all – just green stems.

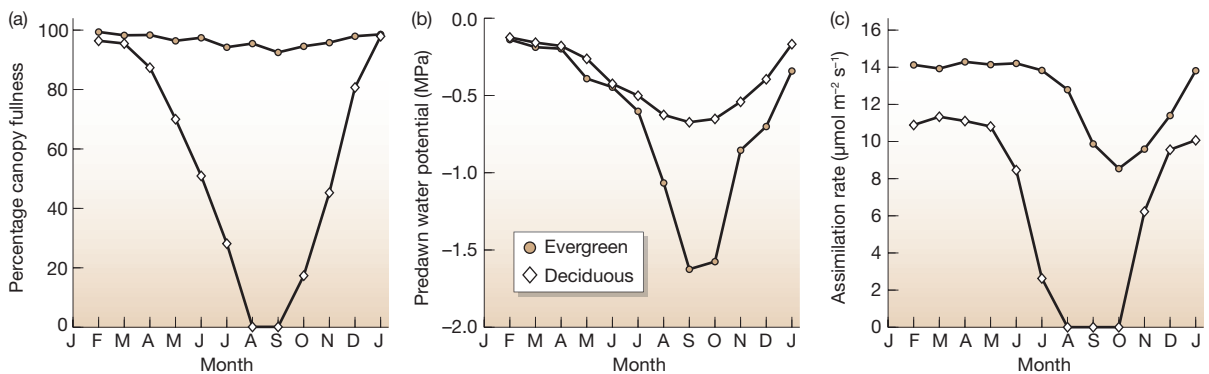
Other plants, *tolerators*, have evolved a different compromise, producing long-lived leaves that transpire slowly (for example, by having few and sunken stomata). They tolerate drought, but of course their photosynthesis is slower. These plants have sacrificed their ability to achieve rapid photosynthesis when water is abundant but gained the insurance of being able to photosynthesize throughout the seasons. This is not only a property of plants from arid areas but also of the pines and spruces that survive where water may be abundant but is usually frozen and therefore inaccessible.

The viability of alternative strategies to solve the problem of photosynthesizing in a dry environment is nicely illustrated by the trees of seasonally dry tropical forests and woodlands. These communities are found naturally in Africa, the Americas, Australia and India; but whereas, for example, the savannas of Africa and India are dominated by deciduous species (losing all leaves for at least 1 and usually 2–4 months each year), and the Llanos of South America are dominated by evergreens (a full canopy all year), in the savannas of Australia there are roughly equal numbers of deciduous and evergreen species (Figure 3.17). The deciduous species avoid drought in the dry season (April–November in Australia) as a result of their vastly reduced rates of transpiration, having shed their leaves (Figure 3.17a, b). The evergreens tolerate the threat of drought in the dry season (Figure 3.17b), but maintain a positive carbon balance throughout the year (Figure 3.17c), whereas the deciduous species make no net photosynthate at all for around 3 months.

The evaporation of water lowers the temperature of the body with which it is in contact. For this reason, if plants are prevented from transpiring they may overheat. This, rather than water loss itself, may be lethal. The desert honey-sweet (*Tidestromia oblongifolia*) grows vigorously in Death Valley, California despite the fact that its leaves are killed if they reach 50°C, a temperature that

coexisting alternative strategies in  
Australian savannas

water and overheating



**Figure 3.17**

(a) Percentage canopy fullness for deciduous and evergreen trees in Australian savannas throughout the year. (Note that the southern hemisphere dry season runs from around April to November.) (b) Susceptibility to drought as measured by increasingly negative values of 'predawn water potential' for deciduous and evergreen trees. (c) Net photosynthesis as measured by the carbon assimilation rate for deciduous and evergreen trees.

is commonly reached in the surrounding air. Transpiration cools the surface of the leaf to a tolerable 40–45°C. Most desert plants bear hairs, spines and waxes on the leaf surface. These reflect a high proportion of incident radiation and help to prevent overheating. Other more general modifications in desert plants include the characteristic ‘chunky’ shape of succulents with few branches, giving a low surface area to volume ratio over which radiant heat is absorbed.

increasing the efficiency of water use: C4 and CAM

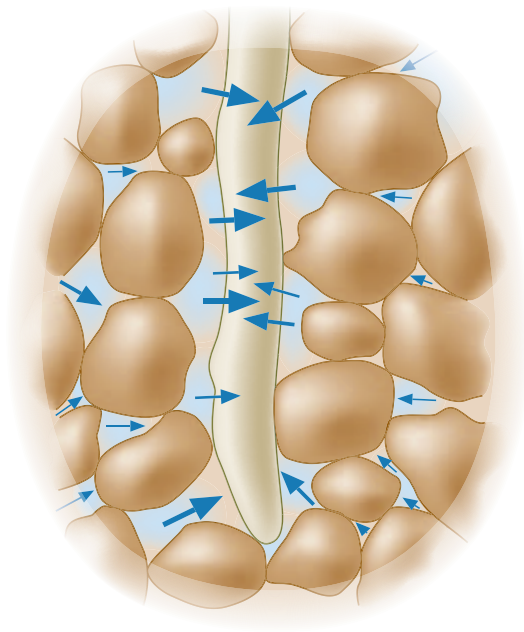
Specialized biochemical processes may increase the amount of photosynthesis that can be achieved per unit of water lost. The majority of plants on Earth photosynthesize using what is termed the *C3 pathway*. Although these plants are highly productive photosynthesizers, they are relatively wasteful of water, reach their maximum rates of photosynthesis at relatively low intensities of radiation, and are less successful in arid areas. Alternative pathways of photosynthesis – termed the *C4 pathway* and *CAM* (crassulacean acid metabolism) – are more economical in their water use. C4 plants have a particularly high affinity for carbon dioxide, and so absorb more per unit of water lost. CAM plants open their stomata at night and absorb carbon dioxide and fix it as malic acid. They close their stomata during the day and release the carbon dioxide internally for photosynthesis. C4 and CAM plants are most common in arid and, in particular, hot arid areas. They are restricted in range because the associated costs of their systems apparently make them less competitive under less arid conditions. For example, the photosynthesis of C4 plants is inefficient at low radiation intensities (see Figure 3.14) and so they are poor shade plants; while CAM plants must store their accumulated malic acid every night: most of them are succulents with extensive swollen water-storage tissues that cope with this problem.

obtaining water from the soil

Almost all falling water (rain, snow, etc.) bypasses the plants and passes to the soil. Some drains through the soil, but much is held against gravity by capillary forces and as colloids. Plants obtain virtually all their water from this stored reserve. Sandy soils have wide pores: these do not hold much water but what is there is held with weak forces and plants can withdraw it easily. Clay soils have very fine pores. They retain more water against the force of gravity, but surface tension in the fine pores makes it more difficult for the plants to withdraw it. The primary water-absorbing zone on roots is covered with root hairs that make intimate contact with soil particles (Figure 3.18). As water is withdrawn from the soil, the first to be released is from the wider pores, where capillary forces retain it only weakly. Subsequent water is withdrawn from narrower paths in which the water is more tightly held. Consequently, the more the soil around the roots is depleted of water, the more resistance there is to water flow. As a result of water withdrawal, roots create water depletion zones (or, more generally, resource depletion zones or RDZs) around themselves. The faster the roots draw water from the soil, the more sharply defined the RDZs, and the more slowly water will move into that zone. In a soil that contains abundant water, rapidly transpiring plants may still wilt because water does not flow fast enough to replenish the RDZs around their root systems (or because the roots cannot explore new soil volumes fast enough).

The shapes of root systems are much less tightly programmed than those of shoots. The root architecture that a plant establishes early in its life can determine its responsiveness to later events. Plants that develop under waterlogged conditions usually set down only a superficial root system. If drought develops later in the season, these same plants can suffer because their root system did not



**Figure 3.18**

Highly diagrammatic picture of a root hair withdrawing water from pores in a very wet soil. Even the widest pores shown are full of water. As water is withdrawn, the wider pores become emptied and water flows only along the twisted pathways through narrower pores.

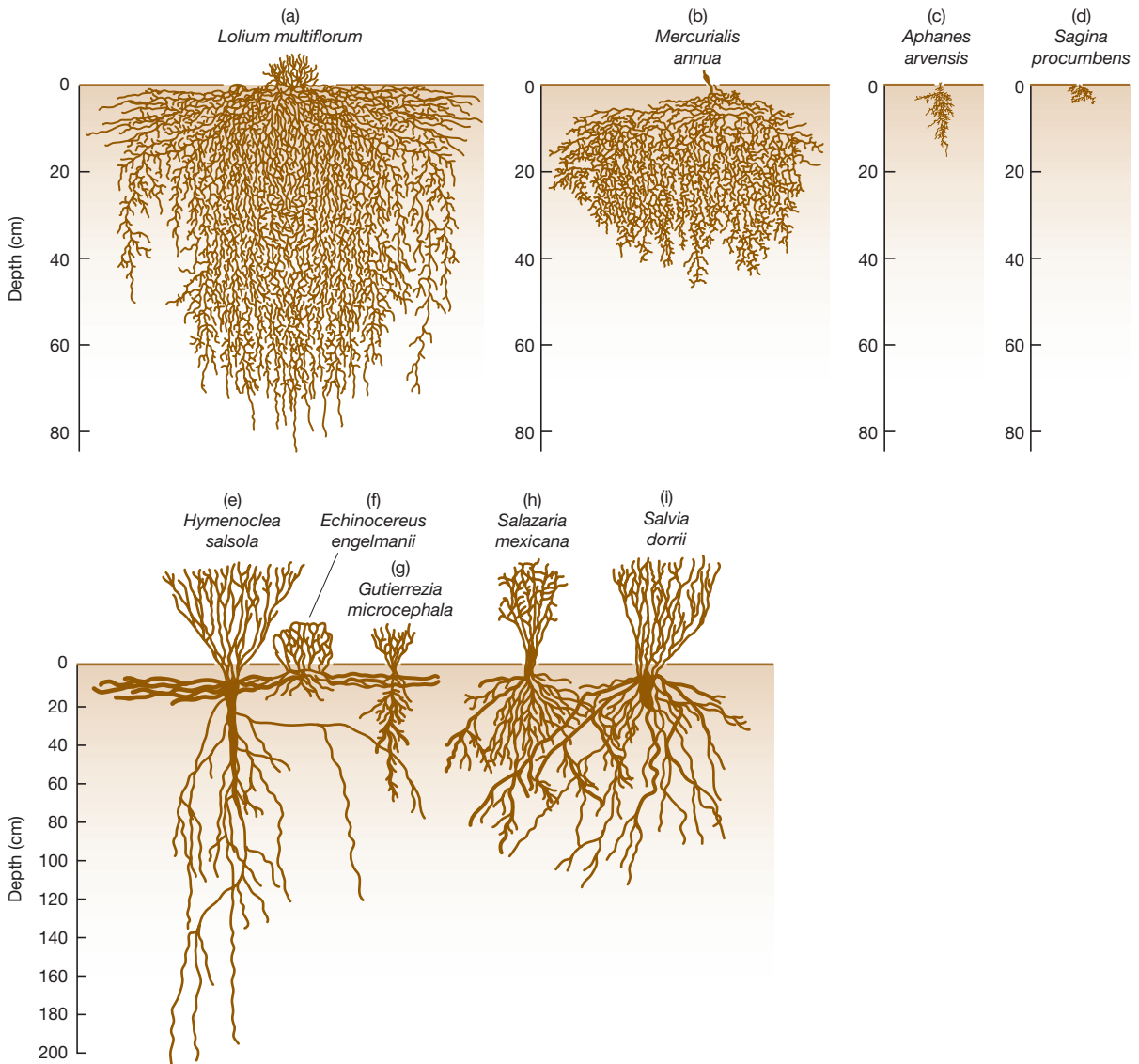
tap the deeper soil layers. A deep tap root, however, will be of little use to a plant in which most water is received from occasional showers on a dry substrate. Figure 3.19 illustrates some characteristic differences between the root systems of plants from damp temperate and dry desert habitats.

### 3.3.3 Mineral nutrients

Roots extract water from the soil, but they also extract key minerals. Plants require mineral resources of nitrogen (N), phosphorus (P), sulfur (S), potassium (K), calcium (Ca), magnesium (Mg) and iron (Fe), together with traces of manganese (Mn), zinc (Zn), copper (Cu) and boron (B). All of these must be obtained from the soil (or directly from the water in the case of free-living aquatic plants). Soils are patchy and heterogeneous, and as roots grow through them, they may meet regions that vary in nutrient and water content. They tend to branch profusely in the richer patches (Figure 3.20).

Root architecture is particularly important in this process, because different nutrients behave differently and are held in the soil by different forces. Nitrate ions diffuse rapidly in soil water, and rapidly transpiring plants may bring nitrates to the root surface faster than they are accumulated in the body of the plant. However, other key nutrients such as phosphate are tightly bound in the soil (have low diffusion coefficients). The phosphate RDZs of two roots 0.2 mm apart scarcely overlap, and the parts of a finely branched root system scarcely compete with each other. Consequently, if phosphate is in short supply, a highly branched surface root will greatly improve phosphate absorption. A more widely spaced extensive root system, in contrast, will tend to maximize access to nitrate.

the architecture of roots determines their foraging efficiency



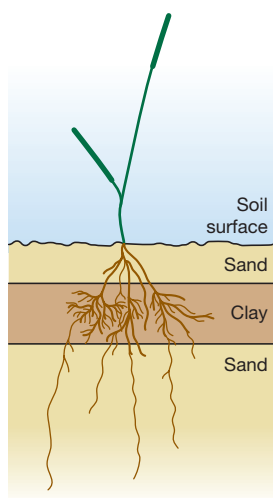
(a–d) FROM FITTER, 1991; (e–i) REDRAWN FROM A VARIETY OF SOURCES

**Figure 3.19**

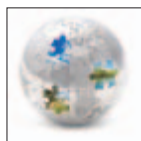
Profiles of root systems of plants from contrasting environments. (a–d) Northern temperate species of open ground: (a) *Lolium multiflorum*, an annual grass; (b) *Mercurialis annua*, an annual weed; and (c) *Aphanes arvensis* and (d) *Sagina procumbens*, both ephemeral weeds. (e–i) Desert shrub and semishrub species, Mid Hills, eastern Mojave Desert, California.

### 3.3.4 Carbon dioxide

Plants take in carbon dioxide through the stomatal pores on leaf surfaces and, as we have seen, using the energy of sunlight, capture the carbon atoms during photosynthesis and release oxygen. Carbon dioxide varies in its concentration at a variety of scales. In 1750, atmospheric carbon dioxide concentrations were approximately  $280 \mu\text{l l}^{-1}$ . Currently, the figure is over  $370 \mu\text{l l}^{-1}$  and is increasing by 0.4–0.5% per year, mainly as a result of the burning of fossil fuels (Box 3.2).

**Figure 3.20**

The root system developed by a young plant of wheat growing through a sandy soil with a layer of clay. Clays offer more nutrient resources and hold more water than sand and the roots respond by branching more intensively in the clay.



## 3.2 Topical ECOncerns

### 3.2 TOPICAL ECONCERNS

#### Global warming? Can we risk it?

Carbon dioxide is one of several global 'greenhouse gases' (see Section 13.3.1), whose increasing concentrations are believed by most scientists to be leading to rises in global mean temperatures, to a growth in the number of 'extreme' and 'record' weather events, and to the threat of the major biomes of Earth substantially changing their distribution (see Box 4.1).

The Intergovernmental Panel on Climate Change (IPCC) was established in 1988 by the World Meteorological Organization (WMO) and the United Nations Environment Programme (UNEP). Each report produced by the IPCC is written by some 200 independent scientists and other experts in approximately 120 countries around the world and is reviewed by another 400 independent experts.

A recent report (IPCC, 2001) describes the current state of understanding of the climate system, providing estimates of future change and highlighting areas of uncertainty. It concludes that an increasing body of observations point to a warming world – temperatures have risen during the past four decades in the lowest 8 km of the atmosphere, global average sea level has

risen, snow cover and ice extent have decreased. These changes have occurred at the same time as atmospheric greenhouse gases continue to increase due to human activities and the panel points to new and stronger evidence that most of the observed warming over the past half century is attributable to human activities. Scientists now have greater confidence in the ability of models to project future climate, and all reasonable scenarios point to a substantial temperature increase. Globally averaged surface temperature is expected to increase by between 1.4°C and 5.8°C in the period 1990 to 2100, with complex consequences for weather patterns and sea level.

Policy-makers and law-makers are faced with different groups of scientific 'experts' offering different projections into the future, and with many interest groups, including a number of industries resisting attempts to force them to change their behavior in order to reduce emissions of greenhouse gases. Even though the majority of scientists believe the problem to be a very real one, the truth is that predictions of the future can never be made with absolute certainty.

Put yourself in the position of a politician. Would it be reasonable of you to demand major changes of significant sectors of the national economy, in order to avert a disaster that may never happen in any case? Or, since the consequences of the 'worst case' and even some of the 'middle of the road' scenarios are so

profound, is the only responsible course of action to minimize risk – to behave as if disaster is certain if we do not change our collective behavior, even though it is not? One alternative might be to wait for better data. But suppose that by the time better data are available it is too late . . .

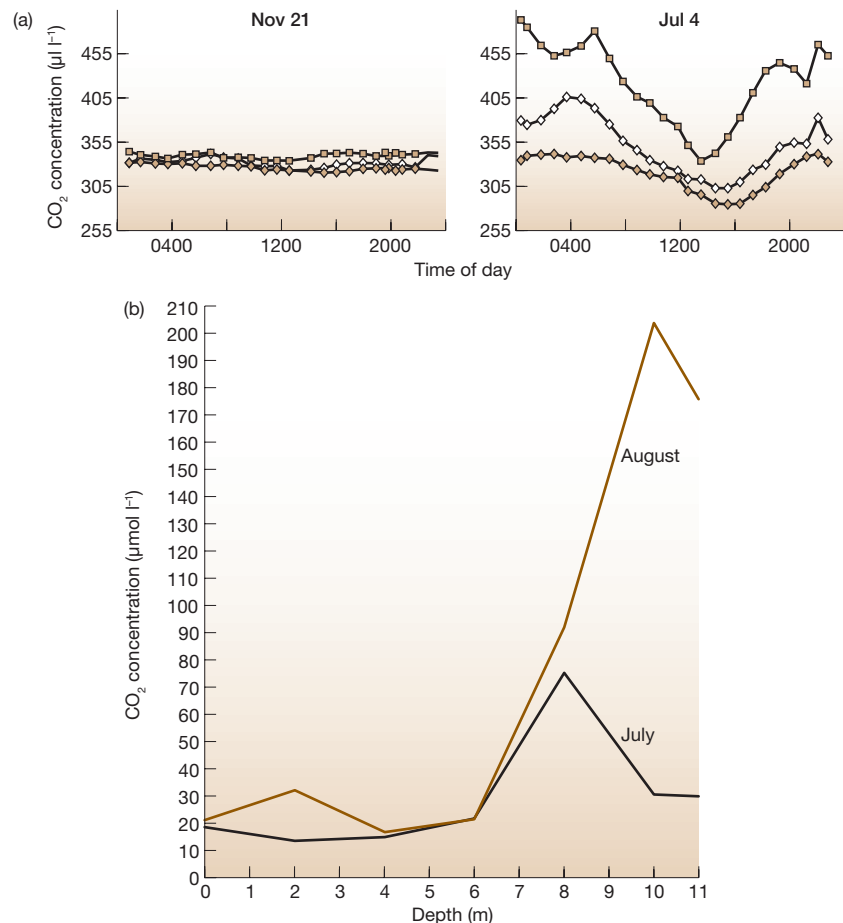
variations beneath a canopy

Plants have responded to even larger fluctuations of carbon dioxide over geological history. During the Triassic, Jurassic and Cretaceous periods, atmospheric concentrations of carbon dioxide were four to eight times greater than at present.

Concentrations can also vary in space and over short time scales. In a terrestrial community (Figure 3.21a), carbon dioxide concentration is highest (up to around  $1800 \mu\text{l l}^{-1}$ ) very close to the ground in summer, where it is released rapidly from decomposing organic matter in the soil. Diffusion alone guarantees that the concentration quickly declines with increasing height, but in the daytime photosynthesizing plants also actively remove carbon dioxide from the air, whereas at night

**Figure 3.21**

(a) Average carbon dioxide concentrations for each hour of the day in a mixed deciduous forest (Harvard Forest, Massachusetts, USA) on November 21 and July 4 at three heights above the ground:  $\blacksquare$ , 0.05 m;  $\diamond$ , 1 m;  $\blacklozenge$ , 12 m. (b) Variation in carbon dioxide concentration with depth in Lake Grane Langsø, Denmark in early July, and also in late August after the lake has become stratified with little mixing between the warm water at the surface and the colder water beneath.



concentrations increase as plants respire and there is no photosynthesis. During the winter, when low temperatures mean that rates of photosynthesis, respiration and decomposition are all slow, concentrations remain virtually constant through day and night at all heights. Thus, plants growing in different parts of a forest will experience quite different carbon dioxide environments: the lower leaves on a forest shrub will usually experience higher carbon dioxide concentrations than its upper leaves, and seedlings will live in environments richer in carbon dioxide than mature trees. In aquatic environments, variations in carbon dioxide concentration can be just as striking, especially when water mixing is limited, for example during the summer ‘stratification’ of lakes, with layers of warm water towards the surface and colder, carbon dioxide-rich layers beneath (Figure 3.21b).

Are higher concentrations of carbon dioxide better for plant growth? When other resources are present at adequate levels, additional carbon dioxide scarcely influences the rate of photosynthesis of C4 plants but increases the rate of C3 plants. Indeed, artificially increasing the carbon dioxide concentration in greenhouses is a commercial technique to increase crop (C3) yields. We might reasonably predict dramatic increases in the productivity of individual plants and of whole crops and natural communities as atmospheric concentrations of carbon dioxide continue to increase. However, there is also much evidence that the responses may be complicated. For example, when six species of temperate forest tree were grown for 3 years in a carbon dioxide-enriched atmosphere in a glasshouse, they were generally larger than controls, but the enhanced growth effect declined even within the relatively short time scale of the experiment (Bazzaz et al., 1993). Moreover, there is a general tendency for carbon dioxide enrichment to reduce the nitrogen concentration in above-ground plant tissues (Cotrufo et al., 1998), which may induce insect herbivores to eat 20–80% more foliage to maintain their nitrogen intake, effectively negating any growth enhancement.

what will be the consequences of current rises?

## 3.4 Animals and their resources

Green plants are *autotrophs*: their resources are quanta of radiation, ions and simple molecules. Plants assemble them into complex molecules (carbohydrates, fats, proteins) and then package them into cells, tissues, organs and whole organisms. It is these packages that form the food resources for virtually all other organisms, the *heterotrophs* (decomposers, predators, grazers, parasites). These consumers unpack the packages, metabolize and excrete some of the contents, and reassemble the remainder into their own bodies. They in turn may be consumed, unpacked and reconstituted in a chain of events in which each consumer becomes, in turn, a resource for some other consumer.

autotrophs and heterotrophs

Heterotrophs can generally be grouped as follows:

- 1 *Decomposers*, which feed on already dead plants and animals.
- 2 *Parasites*, which feed on one or a very few host plants or animals while they are alive but do not (usually) kill their hosts, at least not immediately.
- 3 *Predators*, which, during their life, eat many prey organisms, typically (and in many cases always) killing them.
- 4 *Grazers*, which, during their life, consume parts of many prey organisms, but do not (usually) kill their prey, at least not immediately.

The usual mental image of a predator–prey relationship is something akin to a lion eating a gazelle, but the relationship encompasses a much wider array of consumer–resource interactions. For example, a squirrel is a predator when it eats an acorn (it kills the acorn embryo); a whale is a predator as it feeds on krill; and even a fungus can be regarded as a predator when it feeds on and kills a growing seedling. In each case, the predator kills its food resource as it consumes all or part of it. Here, we concentrate on animal consumers (and take the subject further still in Chapter 7).

#### monophagy and polyphagy

An important distinction between animal consumers is whether they are specialized or generalized in their diet. Generalists (*polyphagous* species) take a wide variety of prey species though they very often have clear preferences and a rank order of what they will choose when there are alternatives available. Specialists, on the other hand, may specialize on particular parts of their prey but range over a number of species. This is most common among herbivores because, as we shall see, different parts of plants are quite different in their composition. Thus, many birds specialize on eating seeds though they are seldom restricted to a particular species. Finally, a consumer may specialize on a single species or a narrow range of closely related species (when it is said to be *monophagous*). Examples are caterpillars of the cinnabar moth (which eat the leaves, flower buds and very young stems of a species of ragwort, *Senecio*) and many species of host-specific parasites.

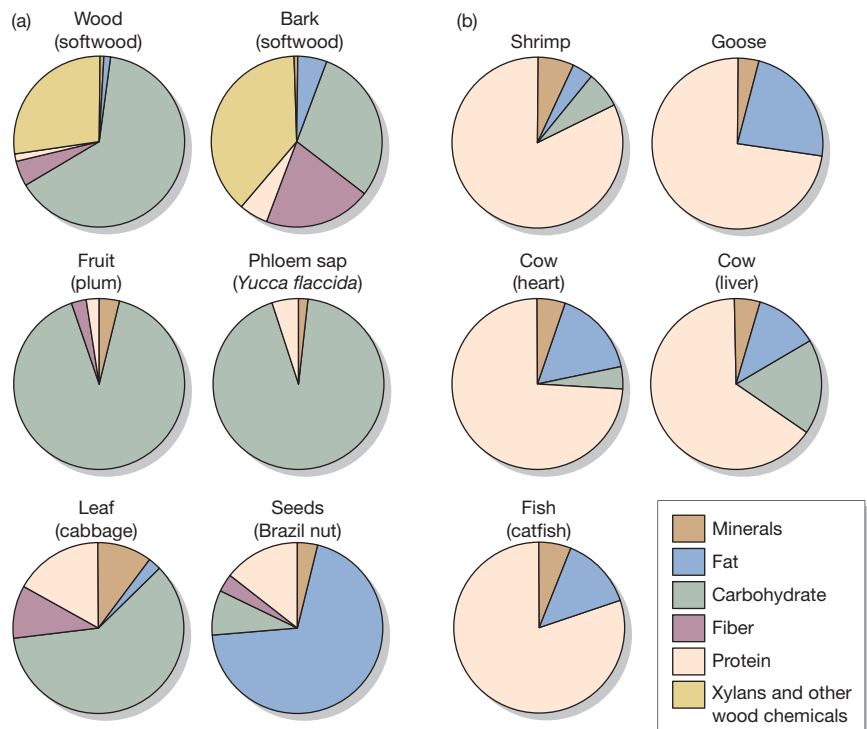
### 3.4.1 Nutritional needs and provisions

#### plants as (a variety of) foods

The various parts of a plant have very different compositions (Figure 3.22a) and so offer quite different resources. Bark, for example, is largely composed of dead

**Figure 3.22**

The composition of various plants (a) and animals (b) that may serve as food resources for herbivores or carnivores. Note that the different parts of a plant have very different compositions, whereas different species of animal (and their parts) are remarkably similar.







**Figure 3.23**

Examples of the variety of specialized mouthparts in herbivorous insects. (a) Honeybee with a long 'tongue' (glossia) for sucking. (b) Hawkmoth with an even longer sucking proboscis. (c) Leichhardt's grasshopper with large, plate-like chewing mandibles. (d) Acorn weevil with chewing mouthparts at the very end of its long rostrum. (e) Rose aphid with a piercing stylet.

(a) © DOUG SOKELL, VISUALS UNLIMITED; (b) © VISUALS UNLIMITED; (c) © MANTIS WILDLIFE FILMS/OXFORD SCIENTIFIC FILMS IOR320MWF001; (d, e) © OXFORD SCIENTIFIC FILMS IC03400SF00501, IHE120PRR00101

cells with corky and lignified walls, packed with defensive phenolics, and is quite useless as a food for most herbivores (even species of 'bark beetle' specialize on the nutritious cambium layer just beneath the bark, rather than on the bark itself). The richest concentrations of plant proteins (and hence of nitrogen) are in the meristem in the buds at shoot tips and in leaf axils. Not surprisingly, these are usually heavily protected with bud scales and defended from herbivores by prickles and spines. Seeds are usually dried, packaged reserves rich in starch or oils as well as specialized storage proteins. And the very sugary and fleshy fruits are resources provided by the plant as 'payment' to animals that disperse the seeds. Very little of the plants' nitrogen is spent on these rewards.

The diversity of different food resources offered by plants is matched by the diversity of specialized mouthparts and digestive tracts that have evolved to consume them. This diversity is especially developed in the beaks of birds and the mouthparts of insects (Figure 3.23).

For a consumer, the body of a plant is a quite different package of resources from the body of an animal. First, plant cells are bounded by walls of cellulose, lignin and other structural carbohydrates that give plants their high fiber content and contribute to their high ratio of carbon to other elements. These large amounts of fixed carbon mean that plants are potentially rich sources of energy. Yet the overwhelming majority of animal species lack cellulolytic and other enzymes that

from plants into animals



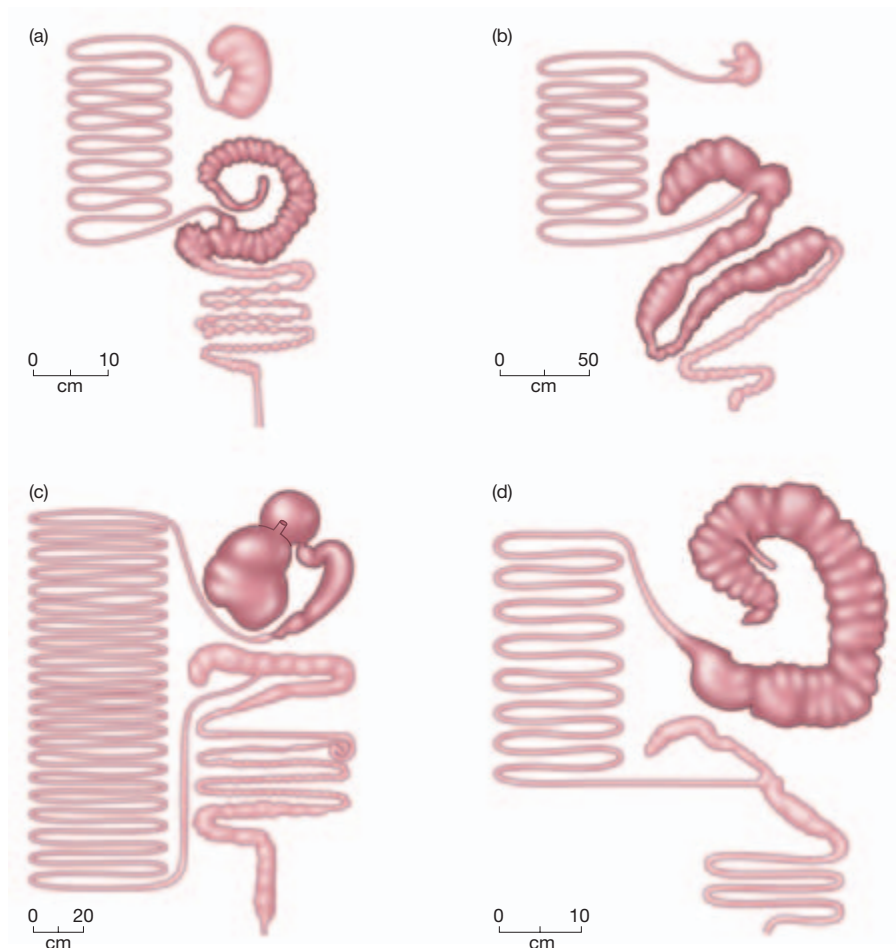
can digest these compounds: they are quite useless as a direct energy resource for most herbivores. Moreover, the cell wall material of plants hinders the access of digestive enzymes to the plant cell contents. The acts of chewing by the grazing mammal, cooking by humans, and grinding in the gizzard of birds are necessary precursors to digestion of plant food because they allow digestive enzymes access to the cell contents. The carnivore, by contrast, can more safely gulp its food.

Many herbivores have made up for their own lack of cellulolytic enzymes by entering into a *mutualistic* (beneficial to both parties) association with cellulolytic bacteria and protozoa in their guts that do have the appropriate enzymes. The rumen (or sometimes the cecum) of many herbivorous mammals is a temperature-regulated culture chamber for these microbes into which already partially fragmented plant tissues flow continually (Figure 3.24). The microbes receive a home and a supply of food. The herbivorous ‘host’ benefits by absorbing many of the major byproducts of this microbial fermentation, especially fatty acids.

Unlike plants, animal tissues contain no structural carbohydrate or fiber component but are rich in fat and protein. The C : N ratio of plant tissues commonly exceeds 40 : 1, in contrast to ratios that rarely exceed 10 : 1 in bacteria, fungi and animals. Thus herbivores, which undertake the first stage of making animal

**Figure 3.24**

The digestive tracts of herbivores are commonly modified to provide fermentation chambers inhabited by a rich fauna and flora of microbes. The figure shows the digestive tracts of four different herbivorous mammals with the fermentation chambers highlighted in a darker shade. (a) Rabbit, with a fermentation chamber in the expanded cecum. (b) Zebra, with fermentation chambers in both cecum and colon. (c) Sheep, with foregut fermentation in an enlarged portion of the stomach, rumen and reticulum. (d) Kangaroo, with an elongate fermentation chamber in the proximal portion of the stomach.



bodies out of plants, are involved in a massive burning off of carbon as the C : N ratio is lowered. The main waste products of herbivores are therefore carbon-rich compounds (carbon dioxide and fiber). Carnivores, on the other hand, get most of their energy from the protein and fats of their prey, and their main excretory products are consequently nitrogenous.

Even if the cell wall is excluded from consideration, the C : N ratio is high in plants compared with other organisms. Aphids, which gain direct access to cell contents by driving their stylets into the phloem transport system, gain a resource that is rich in soluble sugars (see Figure 3.22a). In their search for valuable nitrogen, they use only a fraction of this energy resource and excrete the rest in sugary rich honeydew that may drip as a rain from an aphid-infested tree. For most herbivores and decomposers, the body of a plant is a superabundant source of energy and carbon; it is other components of the diet, especially nitrogen, that are more usually limiting.

The bodies of different species of animal have remarkably similar composition (see Figure 3.22b). In terms of protein, carbohydrate, fat, water and minerals per gram, there is very little to choose between a diet of caterpillars or cod, or of earthworms, shrimps or venison. The packages may be differently assembled (and the taste may be different), but the contents are essentially the same. Moreover, the different parts of an animal have very similar nutritional content. Unlike herbivores, carnivores are not faced with difficult problems of digestion (and they vary very little in their digestive apparatus) but rather with difficulties in finding, catching and overcoming the defenses of their prey.

animals as food

### 3.4.2 Defense

The value of a resource to a consumer is determined not only by what it contains but by how well its contents are defended. Not surprisingly, organisms have evolved physical, chemical, morphological and behavioral defenses against being attacked. These serve to reduce the chance of an encounter with a consumer and/or increase the chance of survival in such encounters. The spiny leaves of holly are not eaten by larvae of the oak egg moth, but if the spines are removed the leaves are eaten quite readily. No doubt similar results would be achieved in equivalent experiments with foxes as predators and de-spined hedgehogs or porcupines as prey. On a smaller scale, many plant surfaces are clothed in epidermal hairs (trichomes) that may keep the smaller predators (such as thrips and mites) away from the leaf surface (Figure 3.25; see also Figure 3.27a).

Any feature of an organism that increases the energy spent by a consumer in discovering or handling it is a defense if, as a consequence, the consumer eats less of it. The thick shell of a nut increases the time that an animal spends extracting a unit of effective food, and this may reduce the number of nuts that are eaten. We have already seen that most green plants are relatively overprovided with energy resources in the form of cellulose and lignin. It may therefore be cheap to build husks and shells around seeds (and woody spines on stems) if these defense tissues contain rather little protein, and if what is protected is far more valuable.

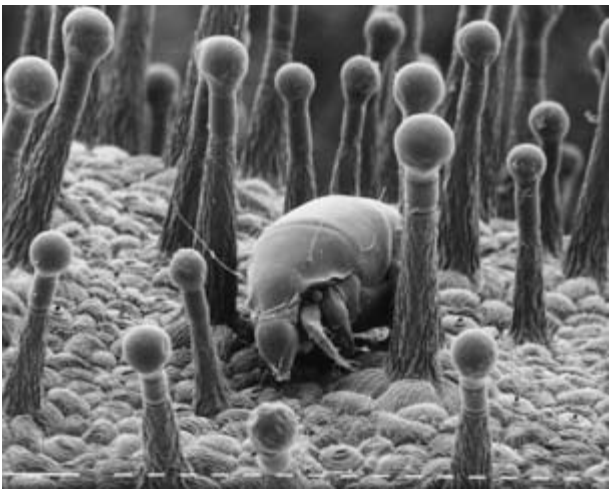
some resources are protected . . .

Both plants and animals have a battery of chemical defenses. The plant kingdom, in particular, is very rich in 'secondary' chemicals that apparently play no role in normal plant biochemical pathways. A defensive function is generally ascribed to these chemicals and a defensive role has been demonstrated

. . . or defended

Figure 3.25

A mite trapped in the protective trichomes (hairs) on the surface of a *Primula* leaf. The trichomes themselves support capsules of irritant volatile oils at their tip. Each white bar towards the foot of the image represents 10  $\mu\text{m}$ .



COURTESY OF C.J. VELTKAMP

optimal defense theory:  
constitutive and inducible  
defenses

unequivocally in some cases. Populations of white clover, for example, commonly contain some individuals that release hydrogen cyanide when their tissues are attacked (*cyanogenic* forms) and others that do not; those that cannot are eaten by slugs and snails. The cyanogenic forms, however, are nibbled but then rejected (Table 3.1).

Noxious plant chemicals have been classified into two broad types. The first are *quantitative* chemicals (so-called because they are most effective at relatively high concentrations), which make the tissues that contain them, such as mature oak leaves, relatively indigestible. They are also often called *constitutive* chemicals, since they tend to be produced even in the absence of herbivore attack. The second type are toxic or *qualitative* chemicals, which are poisonous even in small quantities but can be produced relatively rapidly and are therefore commonly *inducible*: only produced in response to damage itself, and hence with lower fixed costs to the plants.

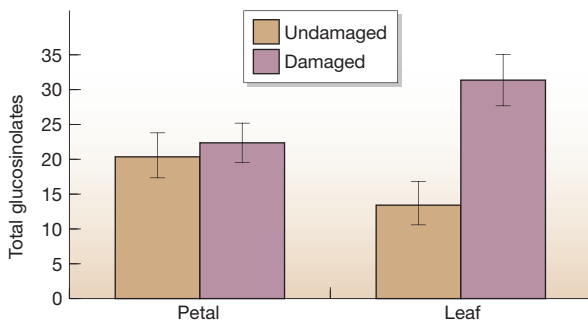
Plants differ in their chemical defenses from species to species and also from tissue to tissue within an individual plant. Broadly, relatively short-lived,

Table 3.1

Slugs (*Agriolimax reticulatus*) graze on the leaves of clover (*Trifolium repens*). There are forms of clover that release hydrogen cyanide when the cells are damaged. Slugs nibble clover leaves and reject cyanogenic forms but continue to consume the leaves of non-cyanogenic forms. Two plants, one of each form, were grown together in plastic containers and slugs were allowed to graze for seven successive nights. The table shows the numbers of leaves in different conditions after slug grazing. +/- indicate deviation from random expectation; the difference from random expectation is significant at  $P < 0.001$ .

	CONDITIONS OF LEAVES AFTER GRAZING			
	NOT DAMAGED	NIBBLED	UP TO 50% OF LEAF REMOVED	MORE THAN 50% OF LEAF REMOVED
Cyanogenic plants	160 (+)	22 (+)	38 (-)	9 (-)
Non-cyanogenic plants	87 (-)	7 (-)	30 (+)	65 (+)

AFTER DIRZO & HARPER, 1982

**Figure 3.26**

Concentrations of glucosinolates ( $\mu\text{g mg}^{-1}$  dry mass) in the petals and leaves of wild radish, *Raphanus sativus*, either undamaged or damaged by caterpillars of *Pieris rapae*. Bars are standard errors.

ephemeral plants gain a measure of protection from consumers because of the unpredictability of their appearance in space and time. They therefore need to invest less in defense than predictable, long-lived species like forest trees. The latter, precisely because they are apparent for long periods to a large number of herbivores, tend to invest in constitutive chemicals that, while costly, afford them broad protection; whereas ephemeral plants tend to produce inducible toxins as required. Moreover, it may be predicted that, within an individual plant, the more important plant parts should be protected by costly, constitutive chemicals, whereas less important parts should rely on inducible toxins (McKey, 1979; Strauss et al., 2004). This is confirmed, for example, by a study of wild radish, in which plants were either attacked by caterpillars of the butterfly, *Pieris rapae*, or left as unmanipulated controls (Figure 3.26). Flower petals are known to be highly important to fitness in this insect-pollinated plant, and concentrations of toxic glucosinolates were twice as high in petals as in undamaged leaves: levels that were maintained constitutively, irrespective of whether the petals were damaged by the caterpillars. Leaves, on the other hand, have a much less direct influence on fitness: high levels of leaf damage can be sustained without any measurable effect on reproductive output. Constitutive levels of glucosinolates, as already noted, were low; but if leaves were damaged, the (induced) concentrations were even higher than in the petals.

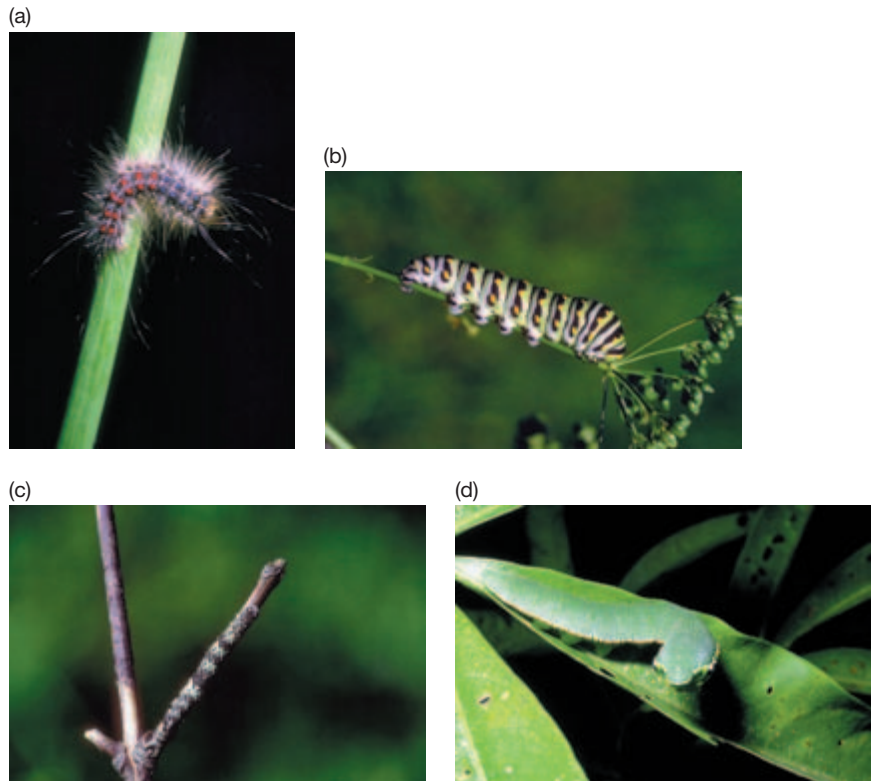
Animals have more options than plants when it comes to defending themselves, but some still make use of chemicals. For example, defensive secretions of sulfuric acid of pH 1 or 2 occur in some marine gastropod groups, including the cowries. Other animals, which can tolerate the chemical defenses of their plant food, actually store the plant toxins and use them in their own defense. A classic example is the monarch butterfly, whose caterpillars feed on milkweeds, which contain cardiac glycosides, which are poisonous to mammals and birds. These caterpillars can store the poison, and it is still present in the adult. Thus, a bluejay will vomit violently after eating one, and, once it recovers, will reject all others on sight. In contrast, monarchs reared on cabbage are edible.

Chemical defenses are not equally effective against all consumers. Indeed, what is unacceptable to some animals may be the chosen, even unique, diet of others. Many herbivores, particularly insects, specialize on one or a few plant species whose particular defense they have overcome. For example, females of the cabbage root fly, with eggs to lay, home in on a brassica crop from distances as far as 15 m downwind of the plants. It is probably hydrolyzed glucosinolates (toxic to many other species) that provide the attractive odor.

chemical defense in animals

**Figure 3.27**

Lepidopterous caterpillars illustrate a range of defense strategies. (a) The irritating hairs of the gypsy moth. (b) Aposematism (advertising distastefulness) in the black swallowtail. (c) A cryptic (camouflaged) noctuid, looking like bark. (d) Another swallowtail rearing and hence possibly startling a potential predator.



crypsis, aposematism,  
and mimicry

An animal may be less obvious to a predator if it matches its background, or possesses a pattern that disrupts its outline, or resembles an inedible feature of its environment. A straightforward example of such *crypsis* is the green coloration of many grasshoppers and caterpillars (Figure 3.27). Cryptic animals may be highly palatable, but their morphological traits and color (and their choice of the appropriate background) reduce the likelihood that they will be used as a resource. In contrast, noxious or dangerous animals often seem to advertize the fact by bright, conspicuous colors and patterns (*aposematism*; Figure 3.27b). The monarch butterfly (see earlier), for example, is aposematically colored. One attempt by a bird to eat an adult monarch is so memorable that others are subsequently avoided for some time. The adoption of memorable body patterns by distasteful prey, moreover, immediately opens the door for deceit by other species – there will be a clear advantage to a palatable prey if it *mimics* an unpalatable species. Thus, the palatable viceroy butterfly mimics the distasteful monarch, and a bluejay that has learned to avoid monarchs will also avoid viceroys.

behavior

By living in holes, animals (millipedes, moles) may avoid stimulating the sensory receptors of predators, and by ‘playing dead’ (opossum, African ground squirrel) animals may fail to stimulate a killing response. Animals that withdraw to a prepared retreat (rabbits and prairie dogs to their burrows, snails to their shells) or roll up and protect their vulnerable parts by a tough exterior (armadillos, hedgehogs) reduce their chance of capture. Other animals seem to try to bluff themselves out of trouble by threatening or startling displays (Figure 3.27d). Moths and butterflies that suddenly expose eye spots on their wings are one example. No

doubt the most common behavioral response of an animal in danger of becoming a used resource is to run away.

### 3.5 Effects of intraspecific competition for resources

Resources are consumed. The consequence is that there may not be enough of a resource to satisfy the needs of a whole population of individuals. Individuals may then compete with each other for the limited resource. *Intraspecific competition* is competition between individuals of the same species.

In many cases, competing individuals do not interact with one another directly. Rather, they deplete the resources that are available to each other. Grasshoppers may compete for food, but a grasshopper is not directly affected by other grasshoppers so much as by the level to which they have reduced the food supply. Two grass plants may compete, and each may be adversely affected by the presence of close neighbors, but this is most likely to be because their resource depletion zones overlap – each may shade its neighbors from the incoming flow of radiation, and water or nutrients may be less accessible than they would otherwise be around the plants' roots. The data in Figure 3.28, for example, show the dynamics of the interaction between a single-celled aquatic plant, a diatom, and one of the resources it requires, silicate. As diatom density increases over time, silicate concentration decreases: there is then less available for the many than there had been previously for the few. This type of competition – in which competitors interact only indirectly, through their shared resources – is termed *exploitation*.

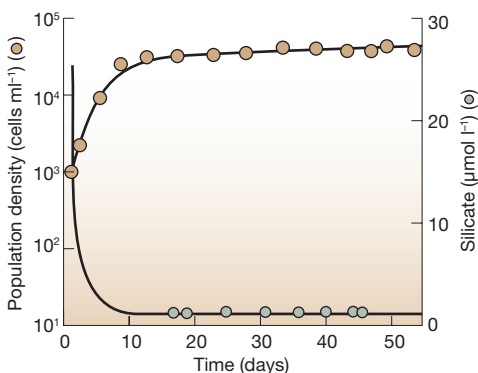
On the other hand, competing individual vultures may fight one another over access to a newly found carcass. Individuals of other species may fight for ownership of a 'territory' and access to the resources that a territory brings with it. A barnacle that settles on a rock denies the space to another barnacle. This is called *interference* competition.

Whether competition occurs through exploitation, interference or a combination of the two, its ultimate effect is on the *vital rates* of the competitors – their survival, growth and reproduction – compared with what they would have been if resources had been more abundant. Competition typically leads to decreased

exploitation: competitors  
depleting each other's resources

direct interference

competition and vital rates



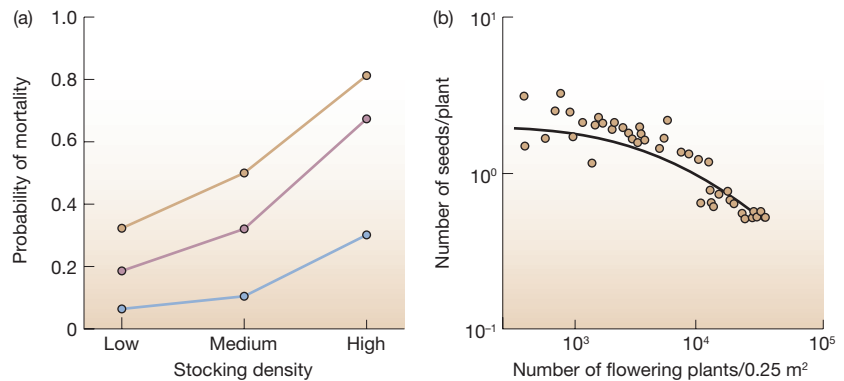
**Figure 3.28**

A population of the freshwater diatom *Asterionella formosa* was grown in flasks of culture medium. The diatom consumes silicate during growth and the population of diatoms stabilizes when the silicate has been reduced to a very low concentration.



Figure 3.29

(a) The rate of mortality among steelhead trout (*Oncorhynchus mykiss*) reared at a range of densities (32, 63 and 127 per m<sup>2</sup>) and at a range of food levels (1.4, 2.9 and 5.8 g of food pellets per day: yellow, maroon and blue lines, respectively). (b) The average number of seeds produced per plant of the dune grass *Vulpia fasciculata* growing at a range of densities.



(a) AFTER KEELEY, 2001; (b) AFTER WATKINSON & HARPER, 1978

rates of resource intake per individual, and thus to decreased rates of individual growth or development, perhaps to decreases in amounts of stored reserves or to increased risks of predation. Figure 3.29a shows how the mortality rate of steelhead trout increases, as the number of competing fish rises, at a range of food levels; Figure 3.29b shows how the birth rate of the sand dune grass *Vulpia* declines as individuals become increasingly crowded.

In practice, intraspecific competition is often a very one-sided affair: a strong early seedling will shade and suppress a stunted, late one; a large vulture is likely to fight off a smaller one. Some of the competitive strength of individuals is related to timing (the early seedling) or to random events (one seed may germinate in a depression where it obtains more water than its neighbors). Sometimes the winner and loser may be genetically different and then competition will be playing a role in natural selection.

The effects of intraspecific competition on any individual are typically greater the more crowded the individual is by its neighbors – the more the resource depletion zones of other individuals overlap its own. This often translates into saying that the greater the density of a population of competitors the greater is the effect of competition. Hence, the effects of intraspecific competition are often said to be *density-dependent*. But it is doubtful that any organism has a way of detecting the density of its population. Rather, it responds to the effects of being crowded.

On the other hand, at low densities in the case of *Vulpia* (Figure 3.29b), the per capita birth rate or fecundity was *independent* of density (where per capita means literally ‘per head’ or ‘per individual’). That is, the fecundity was effectively the same at a density of 1000 plants/0.25 m<sup>2</sup> as it was at a density of 500/0.25 m<sup>2</sup>. Thus, there is no evidence at these densities that individuals are affected by the presence of other individuals and hence no evidence of intraspecific competition. But as density increases further, the per capita birth rate progressively decreases. These effects are now density-dependent, and this may be taken as an indication that at these densities, individuals are suffering as a result of intraspecific competition.

The patterns in Figure 3.29 make the point that as crowding (or density) increases, the fecundity per individual is likely to decline and the mortality per individual likely to increase (which would mean that the survival rate per individual would *decrease*). But what can we expect to happen to the *total* number

density dependence

competition and the total number of survivors



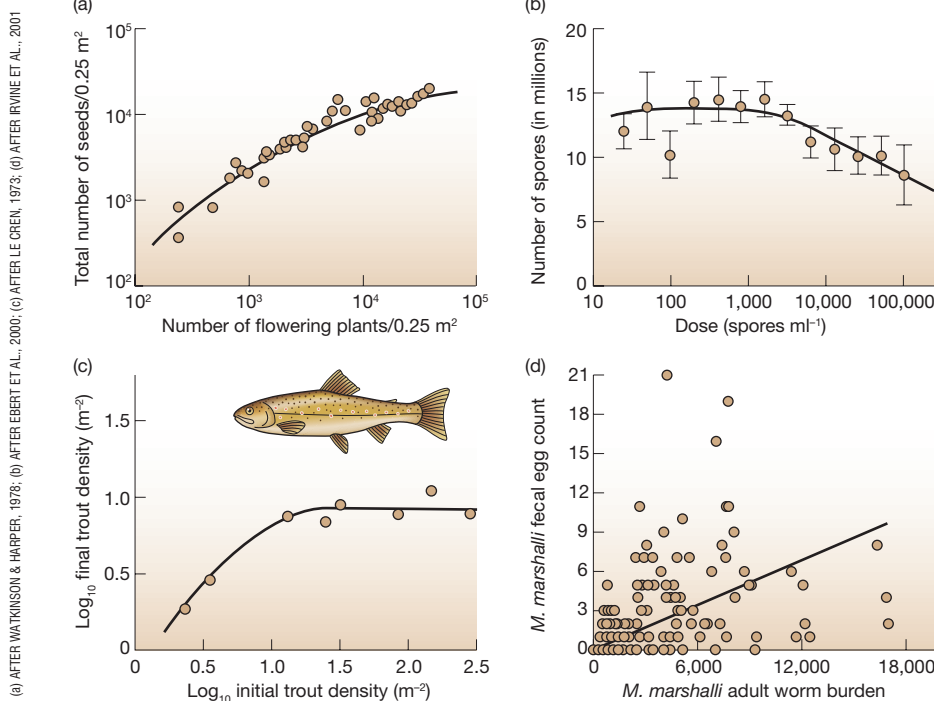


Figure 3.30

Undercompensating, overcompensating and exactly compensating effects of intraspecific competition.

(a) An undercompensating effect on fecundity: the total number of seeds produced by *Vulpia fasciculata* continues to rise as density increases. (b) When the planktonic crustacean *Daphnia magna* was infected with varying numbers of spores of the bacterium *Pasteuria ramosa*, the total number of spores produced per host in the next generation was independent of density (exactly compensating) at the lower densities, but declined with increasing density (overcompensating) at the higher densities. Standard errors are shown. (c) An exactly compensating effect on mortality: the number of surviving trout fry is independent of initial density at higher densities. (d) The total number of eggs of the parasitic nematode *Marshallagia marshalli* produced by infected reindeer (eggs per gram of feces) increased in direct proportion to the number of adult nematodes in the reindeer: there was no evidence of competition between the nematodes.

of seeds or eggs produced by populations at different densities – or to the total number of survivors? In some cases, although the rate per individual declines with increasing density, the total fecundity or total number of survivors in the population continues to increase. This can be seen (Figure 3.30a) to have been the case for the plant populations in Figure 3.29b – at least over the range of densities examined. In other cases, the rate per individual declines so rapidly with increasing density that the total fecundity or total number of survivors in the population actually gets smaller the greater the number of contributing individuals. This can be seen in Figure 3.30b for the highest densities of a bacterial parasite of the planktonic crustacean *Daphnia magna*.

In yet further cases, the mortality risk or fecundity per individual declines with increasing density such that the total number of survivors or total fecundity is the same irrespective of the number of contributing individuals. This is referred to as *exactly compensating density dependence*, and the competition leading to

it is sometimes referred to as ‘contest-like’, since this is the pattern you would expect to see if there were a fixed number of winners and all the other competitors were doomed to lose. Examples are shown for fecundity in Figure 3.30b (at the lower densities) and for survivors in Figure 3.30c. Finally, of course, birth or mortality rates may be density-independent (no competition) throughout the range examined, in which case the total number of births or survivors will simply continue to rise in direct proportion to the original density (e.g. Figure 3.30d).

## 3.6 Conditions, resources and the ecological niche

Finally, many of the ideas in this chapter can be brought together in the concept of the ecological niche. The term *niche*, though, is frequently misunderstood and misused. It is often used loosely to describe the sort of place in which an organism lives, as in the sentence ‘Woodlands are the niche of woodpeckers’. However, strictly, where an organism lives is not its niche but its *habitat*. A niche is not a place but an idea: a summary of the organism’s tolerances and requirements. The habitat of a gut microorganism would be an animal’s alimentary canal; the habitat of an aphid might be a garden; and the habitat of a fish could be a whole lake. Each habitat, however, provides many different niches: many other organisms also live in the gut, the garden, or the lake – and with quite different lifestyles. The niche of an organism describes how, rather than just where, an organism lives.

the niche of an organism is defined by its needs and tolerances

The modern concept of the niche was proposed by Hutchinson in 1957 to address the ways in which tolerances and requirements interact to define the conditions and resources needed by an individual or a species in order to practice its way of life. Temperature, for instance, is a condition that limits the growth and reproduction of all organisms, but different organisms tolerate different ranges of temperature. This range is one *dimension* of an organism’s ecological niche: Figure 3.31a shows how different species of plants vary in the temperature dimension of their niche. But there are many such dimensions for the niche of a species: its tolerance of various other conditions (relative humidity, pH, wind speed, waterflow, and so on), and its need for various resources (nutrients, water, food, and so on). Clearly the real niche of a species must be multidimensional.

It is easy to visualize the early stages of building such a multidimensional niche. Figure 3.31b illustrates the way in which two niche dimensions (temperature and salinity) together define a two-dimensional area that is part of the niche of a sand shrimp. Three dimensions, such as temperature, pH and the availability of a particular food, may define a three-dimensional niche volume (Figure 3.31c). It is hard to imagine (and impossible to draw) a diagram of a more realistic, multi-dimensional niche. (Technically, we now consider a niche to be an *n-dimensional hypervolume*, where *n* is the number of dimensions that make up the niche.) But the simplified three-dimensional version nonetheless captures the idea of the ecological niche of a species. It is defined by the boundaries that limit where it can live, grow and reproduce, and it is very clearly a concept rather than a place. The concept has become a cornerstone of ecological thought, as we shall see in later chapters.

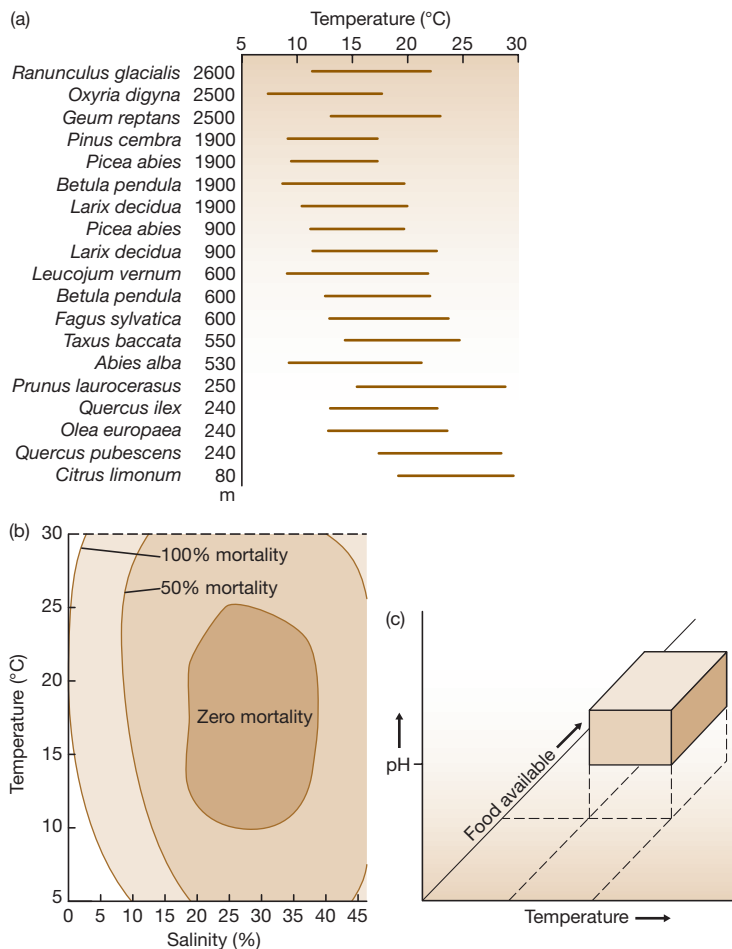


Figure 3.31

(a) A niche in one dimension. The range of temperatures at which a variety of plant species from the European Alps can achieve net photosynthesis at low intensities of radiation ( $70 \text{ W m}^{-2}$ ). (b) A niche in two dimensions for the sand shrimp (*Crangon septemspinosa*) showing the fate of egg-bearing females in aerated water at a range of temperatures and salinities. (c) A diagrammatic niche in three dimensions for an aquatic organism showing a volume defined by the temperature, pH and availability of food.

(a) AFTER PISEK ET AL., 1973; (b) AFTER HAEFNER, 1970



## Summary

### Conditions and resources

Conditions are physicochemical features of the environment such as its temperature and humidity. They may be altered but are not consumed. Environmental resources are consumed by living organisms in the course of their growth and reproduction.

### Environmental conditions

There are three basic types of response curve to conditions. Extreme conditions may be lethal with,

between the two extremes, a continuum of more favorable conditions; or a condition may be lethal only at high intensities; or a condition may be required by organisms at low concentrations but become toxic at high concentrations.

These responses are accounted for, in part, by changes in metabolic effectiveness. But at extremely high temperatures, for example, enzymes and other proteins become unstable and break down, and the organism dies; and at high environmental

temperatures, terrestrial organisms may encounter serious, perhaps lethal, problems of dehydration. At temperatures a few degrees above zero, organisms may be forced into extended periods of inactivity, or ice may form between cells and draw water from within them. The timing and duration of temperature extremes, however, may be as important as absolute temperatures.

In practice, the effects of conditions may be determined largely by the responses of other community members, through food consumption, disease or competition.

Many conditions are important stimuli for growth and development and prepare an organism for conditions that are to come.

### Plant resources

Solar radiation, water, minerals and carbon dioxide are all critical resources for green plants. The shape of the curve that relates the rate of photosynthesis to the intensity of radiation varies greatly among species. The radiation that reaches a plant is forever changing; the plant integrates the diverse exposures of its various leaves.

Most variation in leaf shape has probably evolved under selection to optimize the photosynthesis achieved per unit of water transpired. Any mechanism or process that slows the rate of water loss, such as closing of the stomata, reduces the photosynthetic rate. If the rate of water uptake falls below the rate of release, the body of the plant starts to wilt. If the deficit accumulates, the whole plant may die. Plants may avoid or tolerate water shortage. Specialized biochemical processes may increase the amount of photosynthesis that can be achieved per unit of water lost in C<sub>4</sub> and CAM (as opposed to C<sub>3</sub>) plants.

The primary water-absorbing zone on roots is covered with root hairs that make intimate contact with soil particles. Roots create water depletion zones around themselves. Root architectures are much less tightly programmed than those of shoots, and those established early in a plant's life can determine its responsiveness to later events. Roots also extract key minerals from the soil. Root architecture is particularly

important here because different nutrients are held in the soil by different forces.

### Animals and their resources

Green plants are autotrophs. Decomposers, predators, grazers and parasites are heterotrophs. The various parts of a plant have very different compositions and so offer quite different resources. This diversity is matched by the diversity of mouthparts and digestive tracts that have evolved to consume them. The body of a plant is a quite different package of resources from the body of an animal. To make better use of plant material, many herbivores enter into a mutualistic association with cellulolytic bacteria and protozoa in their alimentary canal.

The C : N ratio of plant tissues greatly exceeds those of bacteria, fungi and animals. Thus, herbivores typically have a superabundant source of energy and carbon, but nitrogen is often limiting; their main waste products are carbon dioxide and fiber. The bodies of different species of animal have remarkably similar compositions. Carnivores are not faced with problems of digestion, but rather with difficulties in finding, catching and overcoming the defenses of their prey. Carnivores' main excretory products are nitrogenous.

### Effects of intraspecific competition for resources

Individuals may compete indirectly, via a shared resource, through exploitation, or directly, through interference. The ultimate effect of competition is on survival, growth and reproduction of individuals. Typically, the greater the density of a population of competitors, the greater is the effect of competition (density dependence). As a result, though, the total number of survivors, or of offspring, may increase, decrease or stay the same as initial densities increase.

### Conditions, resources and the ecological niche

Where an organism lives is its habitat. A niche is a summary of an organism's tolerances and requirements. The modern concept, proposed by Hutchinson in 1957, is an  $n$ -dimensional hypervolume.

## Review questions

### REVIEW QUESTIONS

Asterisks indicate challenge questions

- 1\* Explain, referring to a variety of specific organisms, how the amount of water in different organisms' habitats may define either the conditions for those organisms, or their resource level, or both.
- 2 Discuss whether you think the following statement is correct: 'A layperson might describe Antarctica as an extreme environment, but an ecologist should never do so'.
- 3 In what ways do ectotherms and endotherms differ, and in what ways are they similar?
- 4\* Drawing examples from a variety of both animals and plants, contrast the responses of tolerators and avoiders to seasonal variations in environmental conditions and resources.
- 5 Describe how plants' requirements to increase the rate of photosynthesis and to decrease the rate of water loss interact. Describe, too, the strategies used by different types of plants to balance these requirements.
- 6\* Describe and account for the differences in both root and shoot architecture exhibited by different plants.
- 7 Account for the fact that the tissues of plants and animals have such contrasting C : N ratios. What are the consequences of these differences?
- 8 Describe the various ways in which animals use color to defend themselves against attacks by predators.
- 9 Explain, with examples, what exploitation and interference intraspecific competition have in common and how they differ.
- 10 What is meant when an ecological niche is described as an  $n$ -dimensional hypervolume?

# Chapter 4



## Conditions, resources and the world's communities

### *Chapter contents*

#### CHAPTER CONTENTS

- 4.1 Introduction
- 4.2 Geographic patterns at large and small scales
- 4.3 Temporal patterns in conditions and resources
- 4.4 Terrestrial biomes
- 4.5 Aquatic environments

### *Key concepts*

#### KEY CONCEPTS

In this chapter you will:

- understand that conditions and resources interact to help determine the composition of whole communities
- appreciate that climatic patterns over the surface of the Earth are responsible for the large-scale pattern of distribution of terrestrial biomes (such as tropical rain forest, desert and tundra)
- recognize that biomes are not homogeneous because local topography, geology and soil influence the communities of plants and animals that occur
- appreciate that conditions and resources at a location may change over time scales ranging from hours to millennia, leading to parallel temporal patterns in the composition of communities
- understand that in most aquatic environments it is difficult to recognize anything comparable to terrestrial biomes: communities tend to reflect local conditions and resources rather than global patterns in climate

*The interplay of conditions and resources profoundly influences the composition of the world's communities. At the global scale, patterns of climate circulation are largely responsible for distinctive terrestrial biomes, such as deserts and rain forests, with their characteristic assemblages of plants and animals. Distinct types of marine and freshwater communities can sometimes also be identified at a broad geographic scale. Within each biome or aquatic category, however, there are enormous variations in conditions and resources that are reflected in community patterns viewed at a smaller scale.*

## 4.1 Introduction

Having examined in Chapter 3 the way individual organisms are affected by conditions and resources, we now turn to the larger question of how the interplay of conditions and resources influences whole communities (the assemblages of species that occur together). The answer to this question depends fundamentally on the scale at which we choose to study communities; this will be a pervasive theme throughout the chapter.

Not surprisingly, because of its influence on both conditions and resources, climate plays a major role in determining the large-scale distribution of different types of community across the face of the Earth. However, local factors, such as soil type in terrestrial environments and water chemistry in aquatic environments, are responsible for patchiness in community composition on much smaller scales. We discuss some of the causes of spatial patterns in community distribution in Section 4.2. Then, in Section 4.3, we turn to temporal patterns in conditions and resources that can change community composition over time scales from days to millennia. Section 4.4 describes the characteristics of the Earth's major terrestrial biomes and Section 4.5 deals with the diversity of aquatic communities.

scale and patchiness – central themes of this chapter

## 4.2 Geographic patterns at large and small scales

### 4.2.1 Large-scale climatic patterns

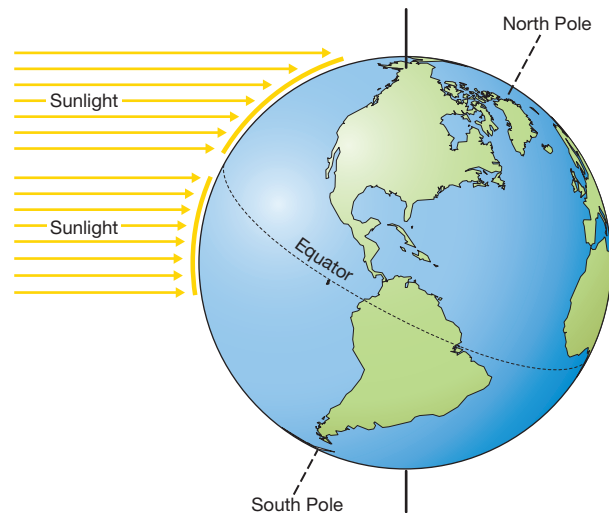
At the largest scale, the geography of life on Earth is mainly a consequence of the planet's movement through space. The tilt of the Earth as it orbits the sun causes solar radiation to strike the Earth's surface with different intensities at different latitudes (Figure 4.1). Because the equator is tilted toward the sun, equatorial and tropical areas receive more direct sunlight and are warmer than other latitudes. Warm air holds more moisture than cold air, increasing the water-holding capacity of air around the tropics. Solar radiation draws water from the vegetation by evaporation, but because the air is so moist, much of the water condenses and

solar radiation, . . .



**Figure 4.1**

The tilt of the Earth on its axis and its rotation around the sun define the amount of radiation striking the atmosphere around the Earth's surface. This, in combination with the daily spin of the Earth on its axis, is responsible for the large-scale patterns of rainfall and solar radiation that define the pattern of global climate. This diagram shows winter in the northern hemisphere with radiation falling almost vertically south of the equator, but the same amount of radiation is spread over greater areas north of the equator; less is therefore received, and there is less heating per unit area.



AFTER AUDESIRK &amp; AUDESIRK, 1996

falls back as rain. Thus, the air that cycles to the atmosphere from the tropics is relatively dry, having lost most of its moisture as local rainfall before it ascends to the lower atmosphere.

The rotation of the Earth causes air masses from the tropics to curve to the north and south. Air that was warmed at the tropics (and which lost moisture as local rain) cools in the atmosphere and descends again at latitudes of approximately 30° (north and south). The air mass warms as it descends, increasing its capacity to hold water and causing the descending air mass to 'soak up' available water from the land. As a result, this is where most of the major deserts, including the Sahara, Kalahari, Mojave and Sonoran, are found. Another smaller evaporation/precipitation system occurs between 30° and 60° latitude, as warm air, now moist, rises and is blown further north or south, respectively. As it cools, the air descends again and rains, producing wetter environments.

Ocean currents have further powerful effects on climatic patterns. Southern waters circulate counterclockwise; they carry cold Antarctic waters up along the western coasts of continents and distribute warmer waters from the tropics along their eastern coasts (Figure 4.2). In the northern hemisphere, currents circulate clockwise, carrying cold Arctic waters along the eastern coasts of continents and returning warm tropical currents along western coasts. The cool, dry climate of eastern South America is an effect of the Antarctic Humboldt current; the relatively dry climate of California is a result of Arctic currents. Conversely, on the eastern side of North America the strong tropical Gulf Stream carries with it warm and moist air far into the Atlantic Ocean, affecting even the climate of Western Europe.

The topography of the land has consequences at an intermediate scale for the pattern of terrestrial climates. As winds meet mountain ranges they are forced up and become cooler as they rise. The cooler air holds less moisture so that water is released (as rain and snow) on the windward slopes of the mountains (the Rockies and Himalayas provide striking examples of this effect). As the air passes over to the leeward sides of the mountains it descends, becomes warmer and now absorbs water. This produces a desiccating effect and causes a *rain shadow* along the leeward slopes (Figure 4.3).

... ocean currents ...

... and mountain ranges ...

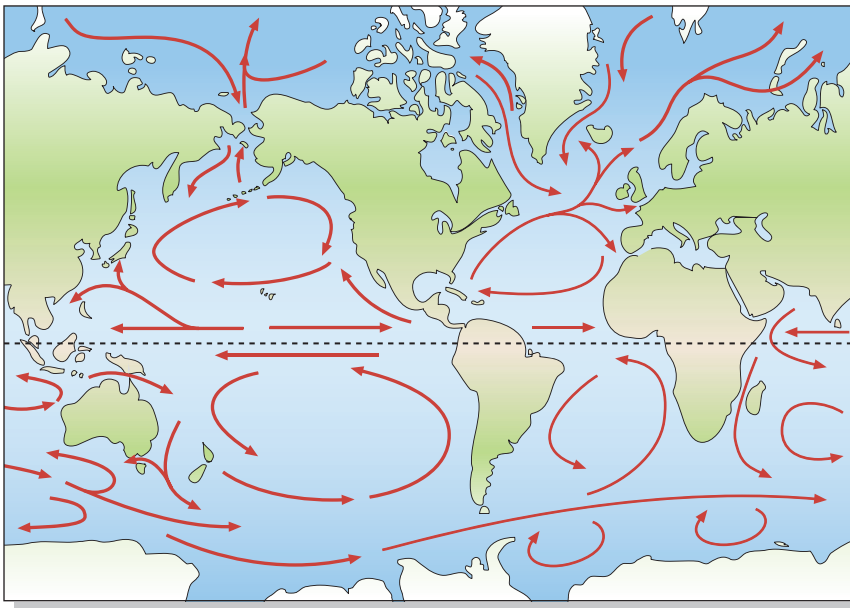


Figure 4.2

The movements of the major ocean currents. The general circulation in the northern hemisphere is clockwise, in the southern hemisphere counterclockwise, with consequences for continental climate patterns.

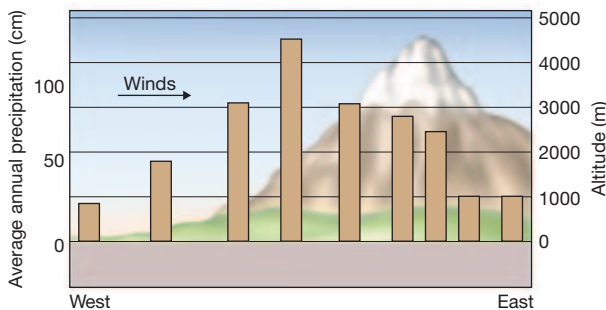


Figure 4.3

The typical influence of topography on rainfall (histogram bars) in the northern hemisphere. Moisture-laden westerlies are forced higher by a mountain range. As they rise they become cooler and release the moisture as rain or snow. This leaves a drier rain shadow on the eastern slopes.

AFTER AUDESIRK & AUDESIRK, 1996

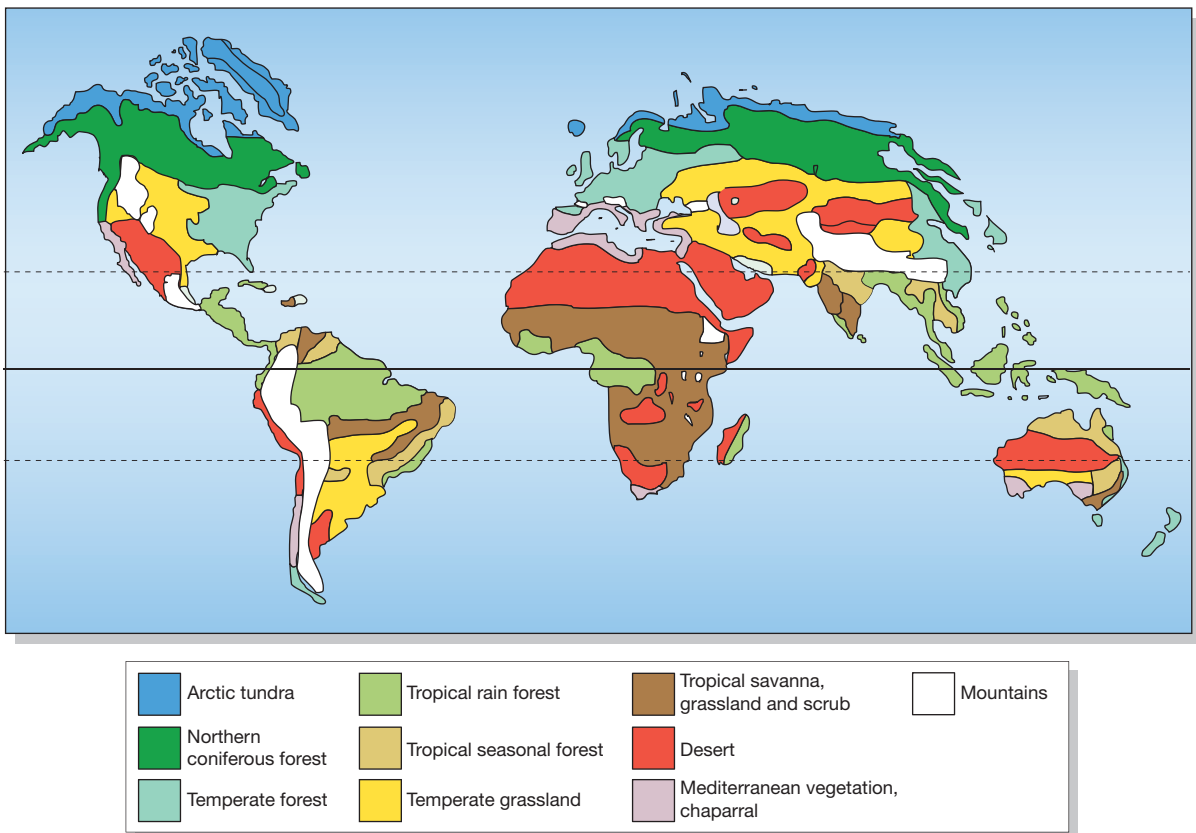
The variety of influences on climate produces a mosaic of dry, wet, cool and warm climates over the surface of the globe. In the patches of this mosaic, distinctive terrestrial associations of vegetation and animals have formed. A world traveler sees repeatedly what can be recognized as characteristic types of vegetation, which ecologists call *biomes* (such as desert, savanna and rain forest). Figure 4.4 recognizes a set of biomes and shows their distribution as a global map. Figure 4.5 shows the ranges of rainfall and mean monthly minimum temperature that are critical in determining where the biomes are found. The characteristics of the communities inhabiting major biomes are described in Section 4.4.

... produce a mosaic of dry, wet, cool and warm climates over the face of the Earth ...

... that, in turn, are responsible for the large-scale distribution of terrestrial biomes

### 4.2.2 Small-scale patterns in conditions and resources

It is easy to be seduced by cartographers who draw sharp lines on maps to show geographic boundaries. But neat pigeonholes, sharp categories and tidy boundaries are a convenience, not a reality of nature. Moreover, biomes are not homogeneous within their hypothetical boundaries; every biome has gradients



**Figure 4.4**

World distribution of the Earth's biomes. Their characteristic plant and animal communities are described in Section 4.4.

of physicochemical conditions related to local topography and geology. The communities of plants and animals that occur in different parts of this heterogeneous patchwork may be quite distinct.

local topography

Local variations in topography can override the broad climatic pattern described in Section 4.2.1. For example, temperature falls with increasing altitude and one effect is that vegetation high on a mountain in the tropics tends to resemble vegetation at low altitudes in northern latitudes. Traveling up a mountain in the tropics involves passing along a similar ecological gradient to that experienced when traveling northward from equator to pole (Figure 4.6).

local geology and soil

It is worth remembering that the Earth's surface would consist of a mosaic of different environments even if climate were identical everywhere. Geological history has provided a variety of rocks that differ in their mineral composition. When the surfaces of these rocks are decomposed by heat, frost and thaw, they give rise to a variety of types of soil that reflect their geological origin. Without soil, it is impossible for significant terrestrial vegetation to grow. Soils provide a source of stored water, a reserve of mineral nutrients, a medium in which atmospheric nitrogen can be fixed for plant use, and the support that allows plants to stand up and expose their leaves to the sunlight.

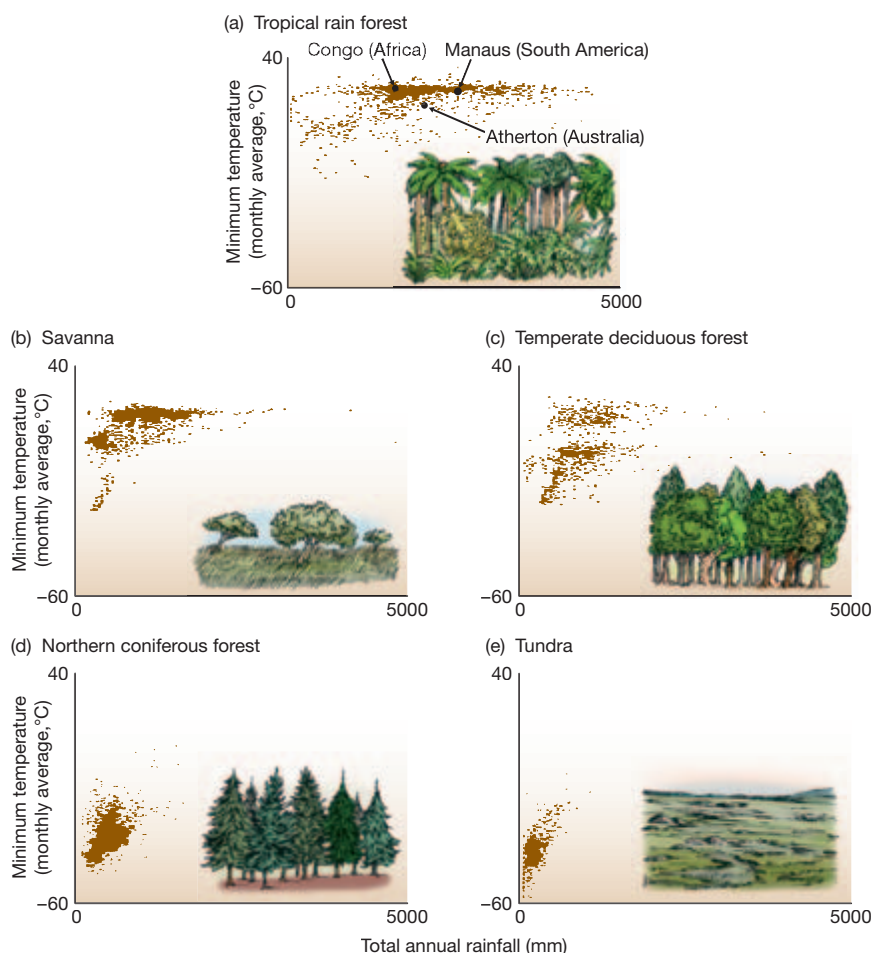


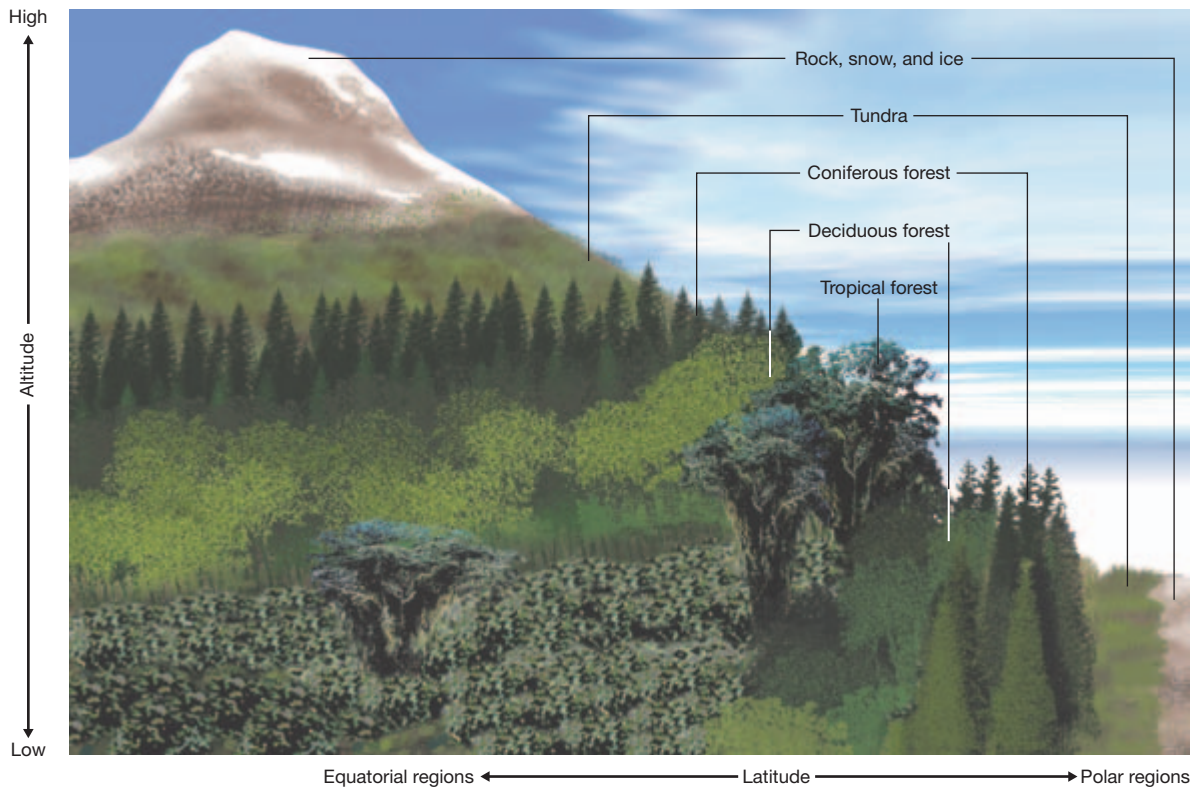
Figure 4.5

The variety of environmental conditions experienced in terrestrial environments can be described in terms of annual rainfall and mean monthly minimum temperatures. The diagrams show the range of conditions experienced in (a) tropical rain forest, (b) savanna, (c) temperate deciduous forest, (d) northern coniferous forest (taiga), and (e) tundra. Data points for a given biome come from different locations around the world. To illustrate this, data points for tropical rain forest on three different continents are shown in (a). Tropical rain forest has characteristically high mean monthly minimum temperatures and high rainfall. In contrast, tundra has both low temperatures and low precipitation. The other biomes occupy intermediate positions in this two-dimensional representation.

Limestone rocks and chalk originated as marine deposits of calcium carbonate, often containing some magnesium and other carbonates. Where these deposits have been raised and exposed as land surfaces they become the basis for neutral or slightly alkaline *calcareous* soils, which bear a characteristic calcium-loving flora. On the other hand, plants normally found on more acid soils, such as *Rhododendron* and *Azalea*, are unsuccessful on calcareous soils. Strict calcium-lovers, in contrast, suffer on acidic soils, where they are intolerant of aluminum ions released at low pH. In the United States, for example, the calcium-loving yellow poplar (*Liriodendron tulipifera*) and northern white cedar (*Thuja occidentalis*) are found only on neutral or alkaline soils, whilst balsam fir (*Abies balsamea*) and eastern hemlock (*Tsuga canadensis*) are usually confined to highly acidic soils.

Variability in the organic matter component of soil also influences the biota that can occur. Organic matter accumulates at different rates in different soils and local variations in the balance between mineral and organic material in the soil contribute to the complexity of environmental mosaics. In extreme conditions, especially where the rocks are acidic, the temperatures are low and/or the soil is waterlogged, the decomposition of organic matter may be seriously impeded.

acidic and calcareous soils bear very different vegetation



**Figure 4.6**

The effect of altitude and latitude on the distribution of biomes. Moving up in altitude is very similar to moving from equator to pole.

patchiness is in the eye of  
the observer . . .

. . . and all communities  
are patchy

Then, peat bogs, with their very specialized plants and animals, form on the partially decomposed organic matter.

To an ecologist, a *patch* in a community is an area in which a single variable distinguishes it from its surroundings. Thus, a fallen tree in a forest leaves a gap in the canopy and a patch on the forest floor where sufficient radiation may penetrate to allow seedlings to grow and eventually fill the gap. A tide pool is a patch on a rocky shore, but within that pool snails may graze and clear a patch free of algae. It is often useful to think of patches as the scale at which particular organisms experience the environment around them. For an aphid in a forest, an individual leaf of a particular species of tree is a patch – it provides both the conditions and the resources necessary for the insect. For a warbler feeding on caterpillars, the canopies of individual trees are patches that it encounters in its daily life. But owls or hawks hunt over a large part of the forest, and for them a patch may be the territory that each bird defends or perhaps even the whole forest over which it ranges.

### 4.2.3 Patterns in conditions and resources in aquatic environments

In most aquatic environments it is difficult to recognize anything comparable to terrestrial biomes. The exceptions occur at the ocean's edge; tropical mangrove swamps, coral reefs and temperate kelp forests have biotas that are as distinctive as

any of the various terrestrial biomes, but this is largely due to their close relationship with major terrestrial climates. In contrast, the open oceans form a continuum in which there is flow of water and dissolved chemicals across the globe. We have seen how variation in the intensity of solar radiation from place to place and between the seasons has dramatic effects on the temperature and water relations of terrestrial environments. But this is not the case in the oceans. The high thermal capacity of water makes the oceans slow to heat and slow to cool. One effect is that the temperature of the water at one point on the globe is a better reflection of where the water has come from (along ocean currents) than of the local climate.

The world's large lakes can be distinguished and classified according to their physical conditions. For example, large lakes in lowland equatorial regions generally experience permanent stratification (distinct layers of water at particular temperatures), whereas seasonal patterns of stratification (in summer) and mixing (in fall) are the rule in temperate regions. Within the polar circles, permanent ice cover with no mixing is characteristic of large lakes. However, local geological conditions and basin size and shape have strong influences on conditions and resources in lakes, particularly in terms of water chemistry, a key determinant of lake flora and fauna. Consequently, a broad geographic classification of lake communities has only limited merit. In the case also of streams, rivers, estuaries and the open ocean, we will see that local conditions and resources are paramount in determining community patterns (see Section 4.5).

### 4.3 Temporal patterns in conditions and resources

The composition of communities can change over time scales ranging from hours to millennia, as conditions and resources themselves change. For example, the microbial community that colonizes and decomposes a dead mouse or fragment of a leaf may change from hour to hour. At the other extreme, we can trace patterns in community composition over tens of thousands of years. Thus, changes in climate during the Pleistocene ice ages bear much of the responsibility for present patterns of distribution of plants and animals. In the 20,000 years since the peak of the last glaciation, global temperatures have risen by about 8°C. Many tree species continue, even today, to migrate northward, following the retreat of the glaciers (Figure 4.7).

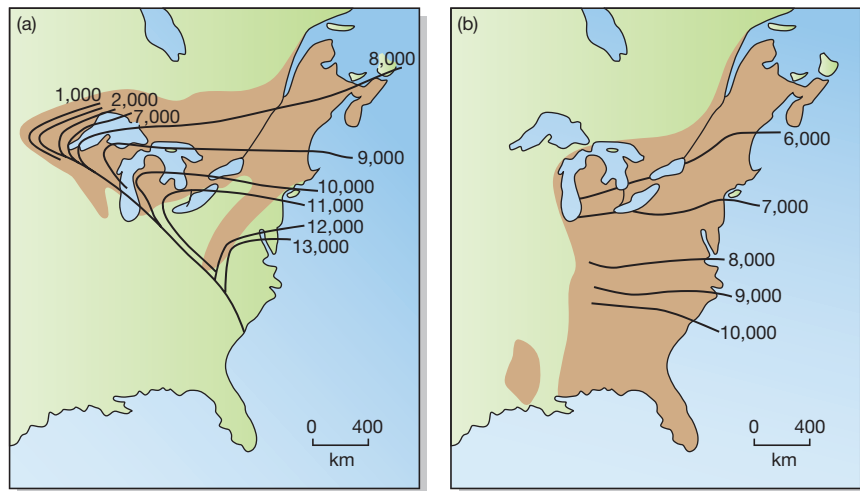
At intermediate temporal scales, predictable sequences of plant species may occur over periods ranging from years to centuries. For example, the successional sequence that occurs on cooled volcanic lava takes several centuries to run its course. This has been documented by comparing the plants living on lava flows from eruptions that occurred at different times on Miyake-jima Island, Japan (Figure 4.8). In the earliest stage of succession, conditions are harsh and soil is sparse and lacking in nitrogen-containing ions, an essential plant resource. Alders are first to colonize because they can fix atmospheric nitrogen into usable form. As nitrogen availability in the soil increases, many species of fern, herb, liana and tree enter the succession. After a century or two, late-successional trees (*Machilus* then *Castanopsis*) shade out many of the earlier arrivals. Succession – the predictable sequence of colonization and extinction after a disturbance – depends partly on changing conditions and resources, and partly on the differential competitive abilities of the plants themselves, a topic we return to in Chapter 9.

plant succession – the species sequence on volcanic lava flows



**Figure 4.7**

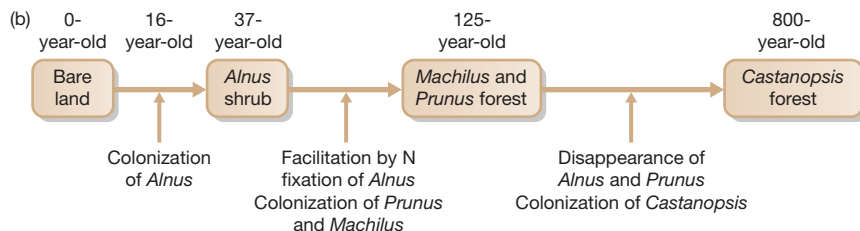
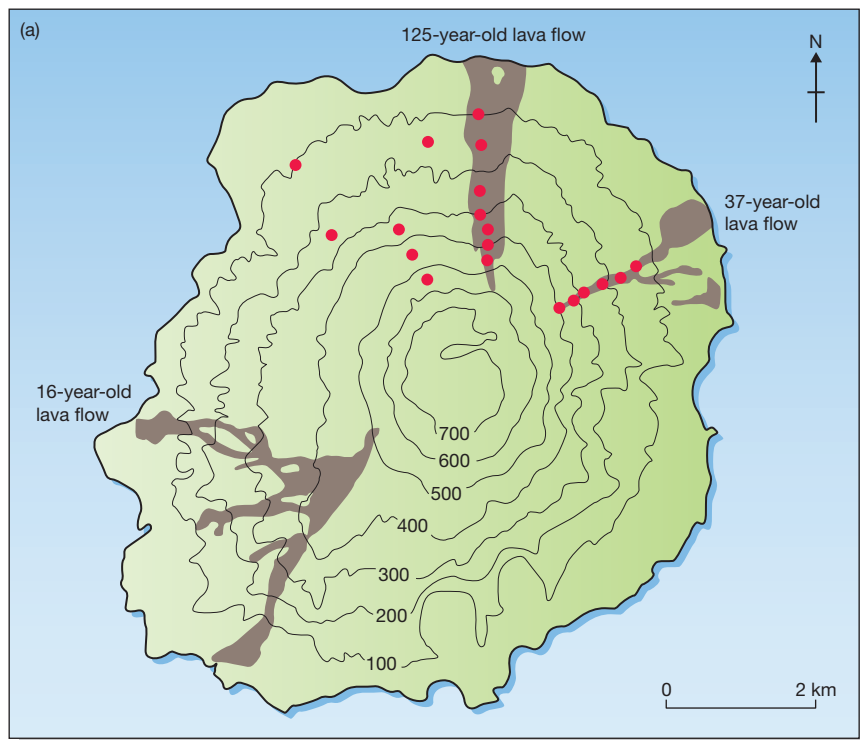
A map showing the spread of two species of forest tree in eastern North America after the retreat of the last ice age glaciation. Note that the two species of (a) eastern white pine (*Pinus strobes*) and (b) beech (*Fagus grandifolia*) have not followed the same invasion path. The lines on the maps (isochrones) define the time of arrival of each species at 1000-year intervals. The numbers on the map refer to thousands of years before present. The shaded brown areas show their present distributions.



FROM DAVIS, 1976

**Figure 4.8**

(a) Locations of sampling sites (red dots) on 37 and 125-year-old lava flows on Miyake-jima Island, Japan. Sampling on 16-year-old lava was non-quantitative (no sampling sites shown). Sites outside these flows are at least 800 years old. Altitudinal contours are shown in meters. (b) In the earliest stage of succession the only vegetation consists of a few small alder trees (*Alnus sieboldiana*). In the older plots (37–800 years old), 113 species were recorded, including ferns, herbs, lianas and trees. This succession consisted of: (i) colonization of the bare lava by the nitrogen-fixing alder; (ii) facilitation (through improved nitrogen availability) of mid-successional *Prunus speciosa* and the late-successional evergreen tree *Machilus thunbergii*; (iii) establishment of a mixed forest in which *Alnus* and *Prunus* were shaded out; and (iv) competitive replacement of *Machilus* by the longer lived *Castanopsis sieboldii*.



AFTER KAMUO ET AL., 2002



## 4.4 Terrestrial biomes

Different biogeographers recognize different numbers of biomes; some make do with just five biomes and others find they need many more. The perspective of the scientist is as important as the system being studied; 'splitters' tend to distrust broad generalizations and emphasize the diversity of the natural world, whereas 'lumpers' force diversity into a minimum of easily mapped categories. The following are adequate for our purposes – tropical rain forest, savanna, temperate grassland, chaparral, desert, temperate deciduous forest, northern or boreal coniferous forest (taiga), and tundra.

the patterns that we recognize in nature depend on how we focus our attention

### 4.4.1 Describing and classifying biomes

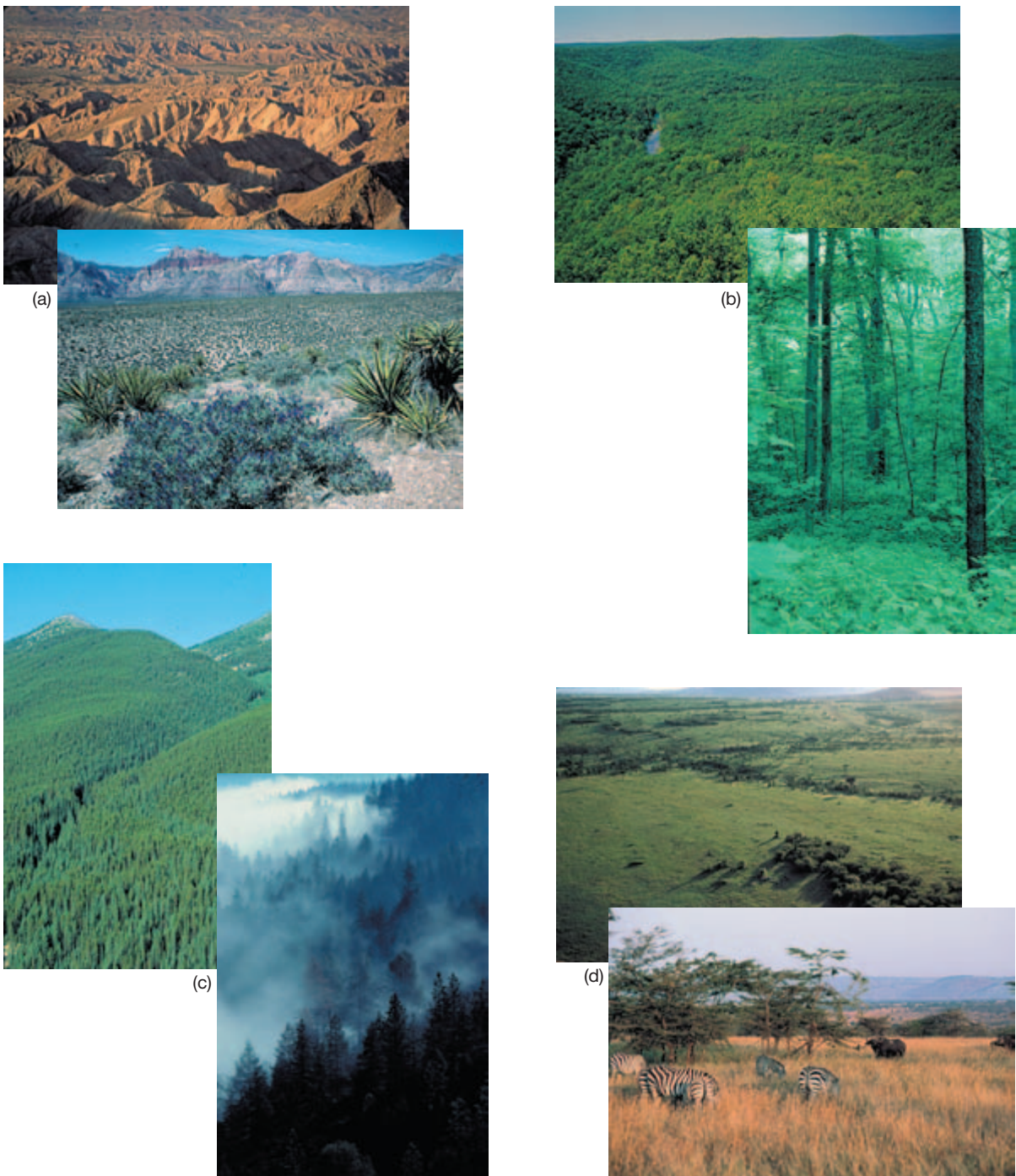
We pointed out in Chapter 2 the crucial importance of geographic isolation in allowing populations to diverge under selection. The geographic distributions of species, genera, families and even higher taxonomic categories of plants and animals often reflect this geographic divergence. All species of lemurs, for example, are found on the island of Madagascar and nowhere else. Similarly, 230 species in the genus *Eucalyptus* (gum tree) occur naturally in Australia (and two or three in Indonesia and Malaysia). The lemurs and the gum trees occur where they do because they evolved there – not because these are the only places where they could survive and prosper. Indeed, many *Eucalyptus* species grow with great success and spread rapidly where they have been introduced to California or to Kenya. A map of the natural world distribution of lemurs tells us quite a lot about the evolutionary history of this group. But as far as its relationship with a biome is concerned, the most we can say is that lemurs happen to be one of the constituents of the tropical rain forest biome in Madagascar.

Another theme of Chapter 2 concerned the way species with quite different evolutionary origins have been selected to converge in their form and behavior. There were also examples of taxonomic groups that have radiated into a range of species with strikingly similar form and behavior (parallel evolution, as in the marsupial and placental mammals). Examples like these reveal much about the ways in which organisms have evolved to match the conditions and resources in their environments. But the different species need not characterize different biomes. Thus, particular biomes in Australia include certain marsupial mammals, while the same biomes in other parts of the world are home to their placental counterparts.

A map of biomes, then, is not usually a map of the distribution of species. Instead, it shows where we find areas of land dominated by plants with characteristic shapes, forms and physiological processes. These are the types of vegetation that can be recognized from an aircraft passing over them or from the windows of a fast car or train. It does not require a botanist to identify them. The scrubby chaparral vegetation characteristic of California provides a striking example. The spectrum of plant forms that gives this vegetation its distinctive nature also occurs in similar environments around the Mediterranean Sea and in Australia – but the species and genera of plants are quite different. We recognize different biomes from the types, not species identities, of organisms that live in them.

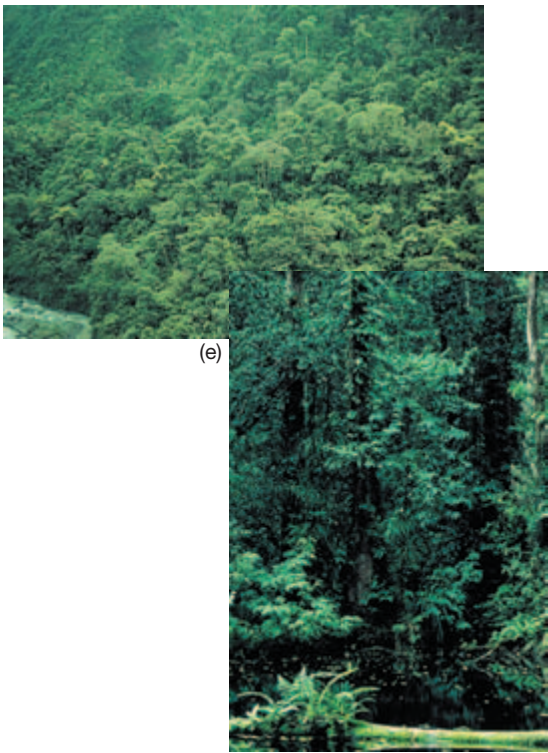
describing and classifying vegetation

When reading the brief descriptions of biomes that follow, it is important to bear in mind that the vegetation described is typical of the mature community that develops in different climatic regions (Figure 4.9). However, patchiness is always

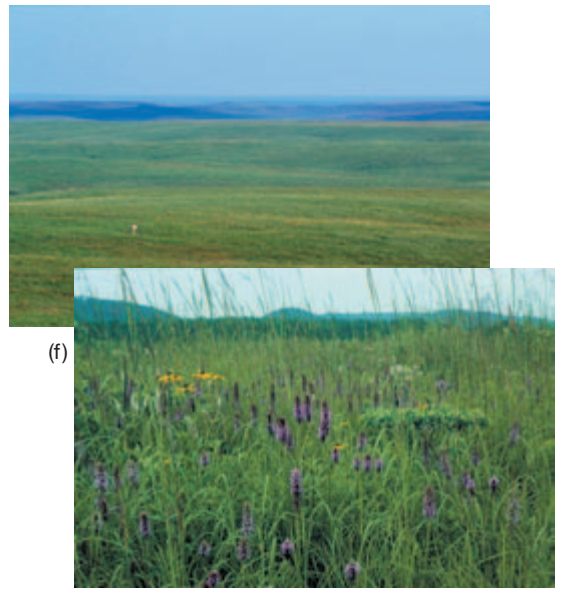


**Figure 4.9**

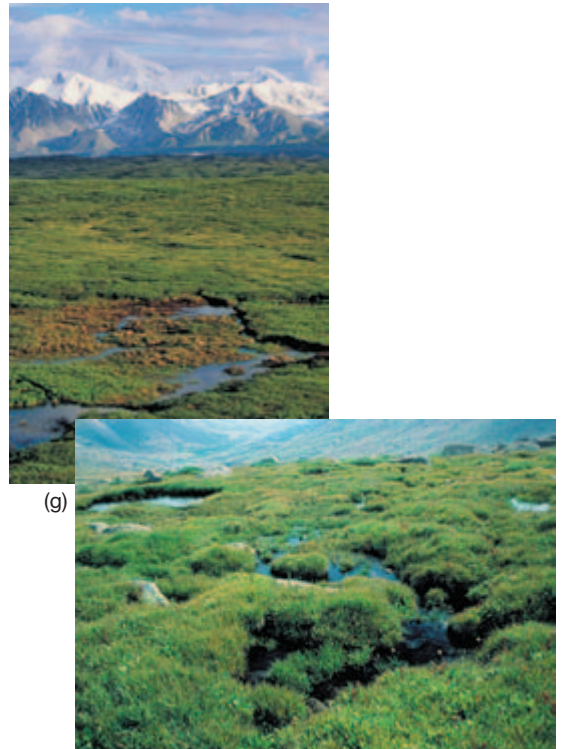
Each biome is illustrated with two photographs, one focusing on the detail of the vegetation and the other providing a distant view and emphasizing the great structural variation to be found among the world's terrestrial communities. The animals found in each of these biomes also cannot be ignored; they are obvious in the savanna photo, but invertebrate and vertebrate animals are busy behind the scenes in all the biomes. (a) Above: Carrizo Badlands desert, Anza-Bonneo Desert State Park, California (© Doug Sokell); below: Red Rock Canyon, Las Vegas, Nevada (© Mark E. Gibson). (b) Above: Ozark Forest and Current River, Ozark National Scenic Riverways, Missouri (© Richard Thom); below: mature eastern deciduous



(e)



(f)



(g)

forest (© Bill Beatty). (c) Above: fir tree forest, Jasper National Park, Alberta, Canada (© Mark E. Gibson); below: foggy coniferous forest, Sierras (© Joe McDonald). (d) Above: Masai Mara Game Preserve at dawn (© Joe McDonald); below: African savanna with zebra and buffalo (© John Cunningham). (e) Above: rain forest, western slope of Andes, Ecuador (© C.P. Hickman); below: lake in mixed dipterocarp forest, Mulu National Park, Sarawak, Borneo (© Brian Rogers). (f) Above: a lone pronghorn antelope looks tiny in this vast mixed-grass prairie, Stanley County, central South Dakota (© Ron Spomer); below: view of prairie in flower with blazing star and black-eyed Susan (© Ann B. Swengel). (g) Above: green tundra with glacial moraine and Alaska mountain range, Denali National Park, Alaska (© Patrick J. Endes); below: wet summer tundra (© Doug Sokel).



present (based often on local topography and geology, Section 4.2.2) and small- and large-scale disturbances (caused by the death of individual trees, or by fires, storms or people) create a mosaic in which community successions are occurring (see Section 4.3).

### 4.4.2 Tropical rain forest

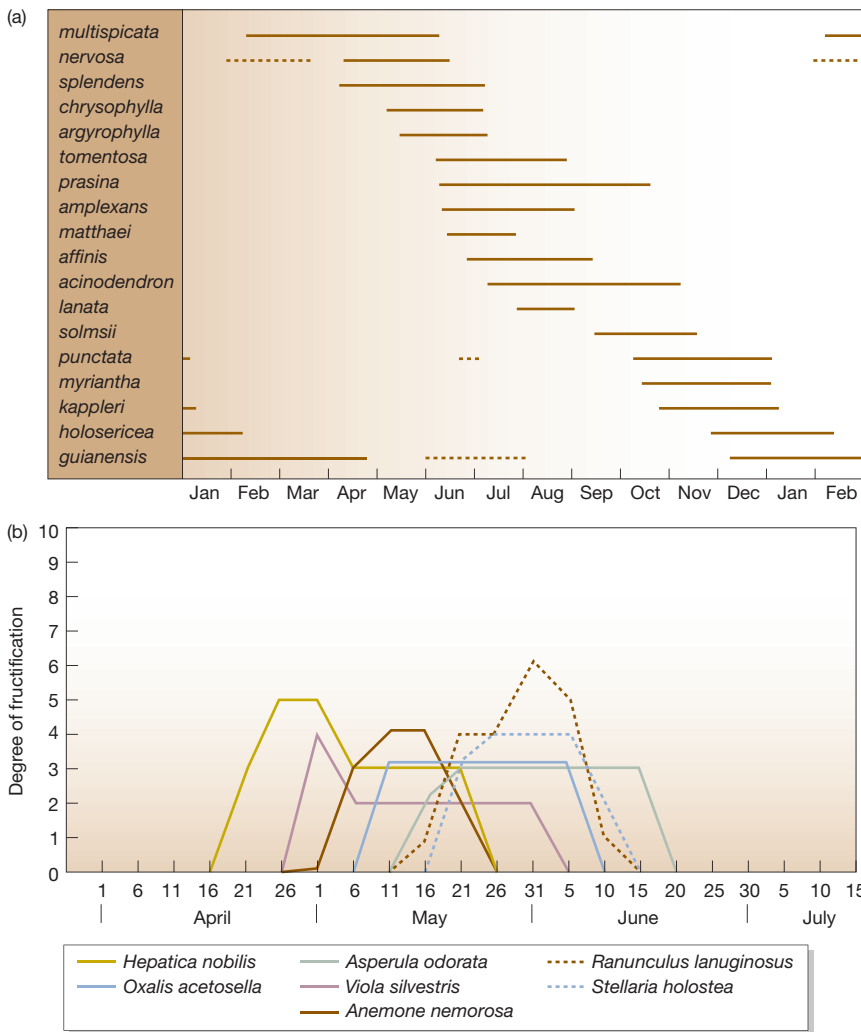
We have chosen to discuss tropical rain forest in greater depth than the other biomes because it represents the global peak of evolved biological diversity: all the other biomes suffer from a relative poverty of resources or more strongly constraining conditions.

Tropical rain forest is the most productive of the Earth's biomes with a photosynthetic productivity that can exceed 1000 g of carbon fixed per square meter per year (see Section 11.2.1). Such exceptional productivity results from the coincidence of high solar radiation received throughout the year and regular and reliable rainfall. The production is achieved, overwhelmingly, high in the dense forest canopy of evergreen foliage. It is dark at ground level except where fallen trees create gaps. A characteristic of this biome is that often many tree seedlings and saplings remain in a suppressed state from year to year and only leap into action if a gap forms in the canopy above them.

Almost all the action in a rain forest (not just photosynthesis but also flowering, fruiting, predation and herbivory) happens high in the canopy. Apart from the trees, the vegetation is largely composed of plant forms that reach up into the canopy vicariously, by climbing the trees (vines and lianas, including many species of fig) or growing as epiphytes, rooted on the damp upper branches. The epiphytes depend on the sparse resources of mineral nutrients that they extract from crevices and pockets of humus on the tree branches. The rich floras and faunas of the canopy are not easy to study; even to gain access to the flowers in order to identify the species of tree is difficult without the erection of tree walks. It is a measure of the problems of doing research in rain forest that botanists have trained monkeys to collect and throw down flowers and a research team has used hot air balloons to move over the canopy and work in it.

Most species of animals and plants in tropical rain forest are active throughout the year, though the plants may flower and ripen fruit in sequence. In Trinidad, for example, the forest contains at least 18 trees in the genus *Miconia*, whose combined fruiting seasons extend throughout the year; this contrasts with the situation in temperate latitudes (Figure 4.10).

Dramatically high species richness is the norm for tropical rain forest (see Section 10.5.2), and communities rarely if ever become dominated by one or a few species – a very different situation from the low biodiversity of northern coniferous forests. This raises some fundamental questions that have proved very difficult to resolve. First, what is it about the evolutionary history of tropical rain forest that has allowed such diversity to evolve? Part of the answer relates to the comparative stability of patches of rain forest during the ice ages. It is thought that during these periods, drought forced tropical rain forests to contract into 'islands' (in a 'sea' of savanna), and these expanded and coalesced again as wetter periods returned. This would have promoted genetic isolation of populations, a phenomenon that is so important for speciation to occur (see Section 2.4). We may also ask why it is that among the diversity of species in tropical rain forests,



AFTER HARPER, 1977

a few have not dominated and suppressed the rest in a struggle for existence. We will see later (Section 10.5.2) that at least part of the answer is that populations of specialized pathogens and herbivores develop near mature trees and attack new recruits of the same tree species nearby. Thus, the chance that a new seedling will survive can be expected to increase with its distance from a mature tree of the same species, reducing the likelihood of dominance by one or a few species in the forest.

The diversity of rain forest trees provides for a corresponding diversity of resources for herbivores (Figure 4.11). A variety of fresh young leaves are available throughout the year, and a constant procession of seed and fruit production provides reliable food for specialists such as fruit-eating bats. Moreover, a diversity of flowers, such as epiphytic orchids with their specialized pollinating mechanisms, require a parallel specialized diversity of pollinating insects. Rain forests are the center of diversity for ants – 43 species have been recorded

tropical rain forest is also associated with high animal diversity . . .

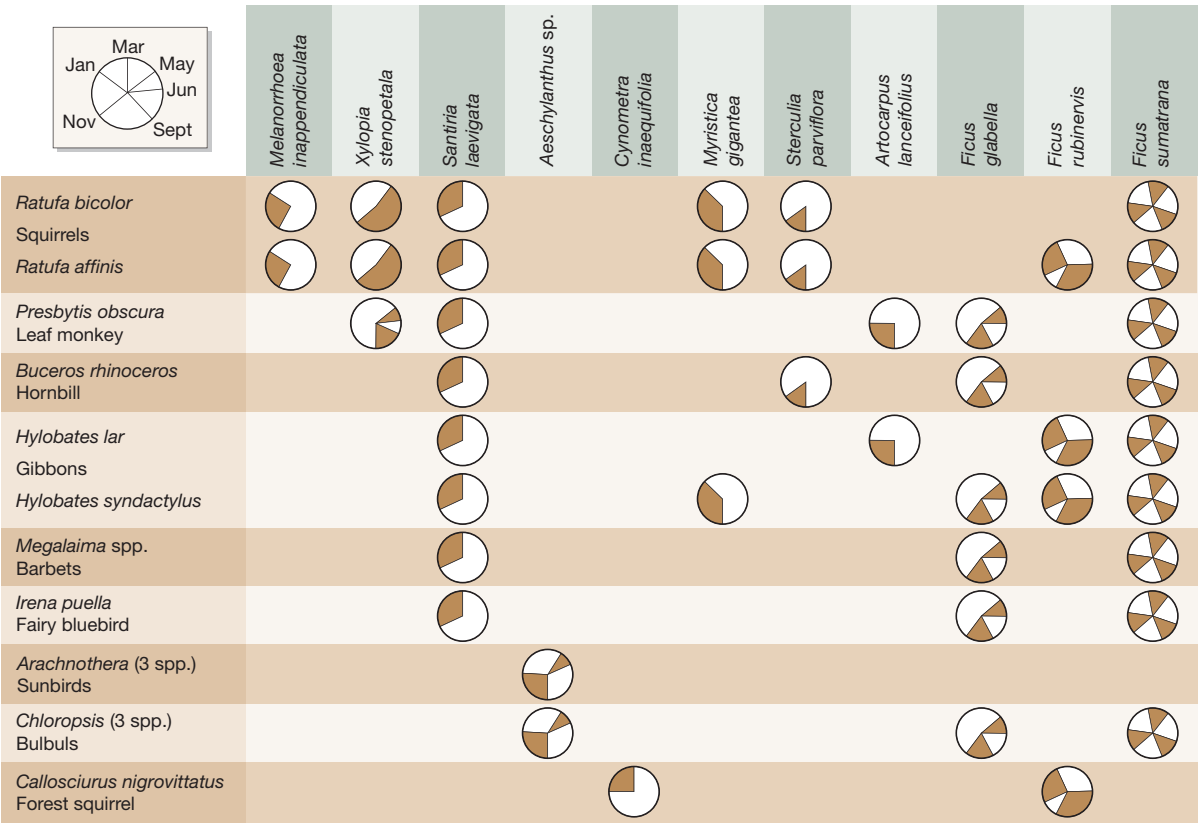


Figure 4.11

Animals (listed vertically) that feed on the fruit of trees (listed horizontally) at various times of the year at Selangor, Malaysia. Each circle is a calendar in which the feeding season is shown in dark brown. Each plant produces fruit only at certain times in the year, but there is fruit available for specialist fruit-eaters throughout the year.

AFTER HARPER, 1977

... and intense soil activity

on a single tree in a Peruvian rain forest. And there is even more diversity among the beetles; Erwin (1982) estimated that there are 18,000 species of beetle in 1 ha of Panamanian rain forest (compared with only 24,000 in the whole of the United States and Canada!).

There is intense biological activity in the soil of tropical rain forests. Leaf litter decomposes faster than in any other biome and as a result the soil surface is often almost bare. The mineral nutrients in fallen leaves are rapidly released, and, as rainfall seeps down the soil profile, nutrients may be carried well below the levels at which roots can recover them. Almost all the mineral nutrients in a rain forest are held in the plants themselves, where they are safe from leaching. When such forests are cleared for agriculture, or the timber is felled or destroyed by fire, the nutrients are released and leached or washed away: on slopes the whole soil may go too. The full regeneration of soil and of a nutrient budget in a new forest may take centuries. Evidence of cultivated patches within rain forest can still be seen clearly from the air 40 years or more after they have been deserted.

All the other terrestrial biomes can be seen as the poor relations of tropical rain forest. They are all colder or drier and all are more seasonal. They have



had prehistories that prevented the evolution of a diversity of animals and plants that approaches the remarkable species richness of tropical rain forest. Moreover, they are generally less suited to the lives of extreme specialists, both plant and animal.

### 4.4.3 Savanna

The vegetation of savanna characteristically consists of grassland with scattered small trees, but extensive areas have no trees. In the absence of other controlling factors, these tropical areas would be expected to be covered by forest. But forest development is kept in check by one of three factors, or a combination of these.

In some savannas, herds of grazing herbivores (e.g. zebra *Equus burchelli* and wildebeest *Connochaetes taurinus* in Africa) have a profound influence on the vegetation, favoring grasses (which protect their embryonic, actively dividing tissues in buds at or just below ground level) and hindering the regeneration of trees (because these same tissues are exposed to browsing animals and to fire).

In other cases, fire is the critical thing. Fire, whether natural or human-induced, can be a common hazard in the dry season and, like grazing animals, tips the balance in the vegetation against trees and favors perennial grasses, with their underground rhizomes and protected regenerating surfaces. In the savannas of Southeast Asia, palms are a feature because scorching of the outermost layer of the trunk does not kill these plants.

Finally, the advantage of grassland over forest in savannas, with their different regional names, may relate to unfavorable conditions, such as water-logging (Venezuelan *llanos*), severe drought (Central American *pine savannas*) or sparse soil nutrients (Brazilian *cerrado*).

Seasonal rainfall places the most severe restrictions on the diversity of plants and animals in savanna. Plant growth is limited for part of the year by drought, and there is a seasonal glut of food, alternating with shortage; as a consequence, the larger grazing animals suffer extreme famine (and mortality) in drier years. The strong seasonality of savanna ecology is well illustrated by its bird populations. An abundance of seeds and insects supports large populations of migrating birds, but only a few species can find sufficiently reliable resources to be resident year round.

seasonal glut and food shortage  
are characteristic of savanna

### 4.4.4 Temperate grasslands

Temperate grassland is the natural vegetation over large areas in every continent. These include the tall grass *prairie* of North America and *pampas* of South America, where rainfall is moderate and soils are rich, and the short grass *steppes* of Russia, typical of more semiarid conditions. These grasslands experience seasonal drought, but grazing animals also have a powerful impact. Populations of invertebrates, such as grasshoppers, are often very large and their biomass may exceed that of grazing vertebrates. The latter include bison (*Bison bison*), pronghorn antelope (*Antilocapra americana*) and gophers (*Thomomys bottae*) in North America, and saiga antelope (*Saiga tatarica*) and marmots (*Marmota bobac*) in Russia.

of all the biomes, temperate grassland has been most transformed by humans

Many of these natural grasslands have been cultivated and replaced by arable annual ‘grasslands’ of wheat, oats, barley, rye and corn. Such annual grasses of temperate regions, together with rice in the tropics, provide the staple food of human populations worldwide. In fact, the vast increase in the size of the human population in historical times (see Section 12.2) has depended on the domestication of grasses for human food or feed for domestic animals. At the drier margins of the biome, where cultivation is not economical, many of the grasslands are ‘managed’ for meat or milk production, sometimes requiring a nomadic human lifestyle. The natural populations of grazing animals, especially bison and pronghorns in North America and ungulates in Africa, have been driven back in favor of cattle, sheep and goats. Of all the biomes, this is the one most coveted, used and transformed by humans.

#### 4.4.5 Desert

In their most extreme form, the hot deserts are too arid to bear any vegetation; they are as bare as the cold deserts of Antarctica. Where there is sufficient rainfall to allow plants to grow in arid deserts, its timing is always unpredictable.

contrasting patterns of behavior of desert plants

Desert vegetation falls into two sharply contrasted patterns of behavior. Many species have an opportunistic lifestyle, stimulated into germination by the unpredictable rains (physiological ‘internal’ clocks are useless in this environment). They grow fast and complete their life history by starting to set new seed after a few weeks. These are the species that can occasionally make a desert bloom; the ecophysiological Fritz Went called them ‘belly plants’ because only someone lying on the ground can appreciate their individual charm.

A different pattern of behavior of arid desert plants is to be long-lived with sluggish physiological processes. Cacti and other succulents, and small shrubby species with small, thick and often hairy leaves, can close their stomata (pores through which gas exchange takes place) and tolerate long periods of physiological inactivity. In arid deserts, freezing temperatures are common at night and tolerance of frost is almost as important as tolerance of drought.

animal diversity is low in deserts

The relative poverty of animal life in arid deserts reflects the low productivity of the vegetation and the indigestibility of much of it. Desert perennials including species of wormwood (*Artemisia*) and creosote plant (*Larrea mexicana*) in the southwestern United States, and mallee species of *Eucalyptus* in Australia, carry high concentrations of chemicals that are repellent to herbivores. Ants and small rodents rely on seeds as a relatively reliable perennial resource, whereas bird species are largely nomadic, driven by the need to find water. Only desert carnivores can survive on the water they obtain from their food. In the deserts of Asia and Africa, camels, donkeys and sheep are managed for transport and food by migrant groups of humans.

#### 4.4.6 Temperate forest

Like all biomes, temperate forest includes, under one name, a variety of types of vegetation. At its low-latitude limits in Florida and New Zealand, winters are mild, frosts and droughts are rare, and the vegetation largely consists of

broad-leaved evergreen trees. At its northern limits in the forests of Maine and the upper Midwest of the United States, the seasons are strongly marked, winter days are short and there may be 6 months of freezing temperatures. Deciduous trees, which dominate in most temperate forests, lose their leaves in the fall and become dormant after transferring much of their mineral content to the woody body of the tree. On the forest floor, diverse floras of perennial herbs often occur, particularly those that grow quickly in the spring, before the new tree foliage has developed.

All forests are patchy because old trees die, providing open environments for new colonists. This patchiness is on an especially large scale after hurricanes fell the older and taller trees or after fire kills the more sensitive species. In temperate forests the canopies are often composed of a mixture of long-lived species, such as red oaks (*Quercus rubra*) in the Midwest of the United States, and colonizers of gaps, such as sugar maple (*Acer saccharum*).

Temperate forests provide food resources for animals that are usually very seasonal in their occurrence (compare Figure 4.10b with 4.10a), and only species with short life cycles, such as leaf-eating insects, can be dietary specialists. Many of the birds of temperate forests are migrants that return in spring but spend the remainder of the year in warmer biomes.

Soils are usually rich in organic matter that is continually added to, decomposed and churned by earthworms and a rich community of other *detritivores* (organisms that feed on dead organic matter). Only waterlogging and low pH, in some locations, inhibit the decomposition of organic matter and force it to accumulate as peat.

Large swathes of deciduous forest in Europe and the United States have been cut down to provide for agriculture, but these have sometimes been allowed to regenerate as farmers abandoned the land (a conspicuous feature in New England).

temperate forest soils are rich in organic matter

#### 4.4.7 Northern coniferous forest (taiga) grading into tundra

Northern (or boreal) coniferous forest (also known as taiga) and the treeless tundra occur in regions where the short growing season and the cold of winter limit the vegetation and its associated fauna.

Coniferous forest consists of a very limited tree flora. Where winters are less severe, the forests may be dominated by pines (*Pinus* species, which are all evergreens) and deciduous trees such as larch (*Larix*), birch (*Betula*) or aspens (*Populus*), often as mixtures of species. Farther north, these species give way to monotonous single-species forests of spruce (*Picea*) over immense areas of North America, Europe and Asia. This provides an extreme contrast to the biodiversity of tropical rain forests.

The areas of vegetation now occupied by tundra and northern coniferous forests (and much of northern deciduous forest) were occupied by the ice sheet during the last ice age, which only started to withdraw 20,000 years ago. Temperatures are now as high as they have ever been since that time, but the vegetation has not yet caught up with the changing climate and the forests are still spreading

the low diversity of northern coniferous forest provides ideal conditions for pest outbreaks

north. The very low diversity of northern floras and faunas is in part a reflection of a slow recovery from the catastrophes of the ice ages.

Low-diversity communities provide ideal conditions for the development of disease and epidemics of pests. For example, the spruce budworm (*Choristoneura fumiferana*) lives at low densities in immature northern forests of spruce. As the forests mature, the budworm populations explode in devastating epidemics. These wreck the old forest, which then regenerates with young trees. This cycle takes about 40 years to run its course.

The overriding environmental constraint in northern spruce forests is the presence of permafrost: the water in the soil remains frozen throughout the year, creating permanent drought except when the sun warms the very surface. The root system of spruce can develop in the superficial soil layer, from which the trees derive all their water during the short growing season.

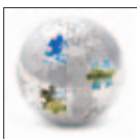
To the north of the spruce forest, the vegetation changes to tundra, with its low shrubs, grasses, sedges and small flowering plants, as well as mosses and lichens. In fact, forest and tundra often form a mosaic in the Low Arctic. In the colder areas, plants such as grasses and sedges disappear, leaving nothing rooted in the permafrost. High winds exaggerate the aridity of the environment, and ultimately vegetation that consists only of lichens and mosses gives way, in its turn, to the polar desert. The number of species of higher plants (i.e. excluding mosses and lichens) decreases from 600 species in the Low Arctic of North America to 100 species in the High Arctic (north of 83°) of Greenland and Ellesmere Island. In contrast, the flora of Antarctica contains only two native species of vascular plant and some lichens and mosses that support a few small invertebrates. The biological productivity and diversity of Antarctica are concentrated at the coast and depend almost entirely on resources derived from the sea.

dramatic animal population cycles are characteristic of northern biomes

The faunas of northern coniferous forests and tundra have intrigued ecologists because populations of lemmings, mice, voles and hares (herbivores), and the fur-bearing carnivores (e.g. lynx and ermine) that feed on them, pass through remarkable cycles of expansion and collapse (see Section 7.5.2). Lemmings (*Lemmus*) are famous for their population cycles and the role they play in the tundra. When the snow melts during a period when the lemming cycle is at a high point, the animals are exposed and they support large migratory populations of predatory birds (owls, skuas, gulls) and mammals such as weasels. Reindeer and caribou (they are the same species, *Rangifer tarandus*) occur in migrant herds capable of foraging on lichens of the tundra, which they can reach through the snow cover.

#### 4.4.8 The future distribution of biomes

It is clear that the distribution of biomes has changed in the past in response to the ebb and flow of the ice ages. Nowadays, we are also acutely aware that their boundaries are probably on the move again. Predicted changes in global climate over the next few decades can be expected to result in dramatic changes to the distribution of biomes over the face of the Earth (Box 4.1). But the exact nature of these changes remains uncertain.



## 4.1 TOPICAL ECONCERNS

### 4.1 Topical ECONcerns

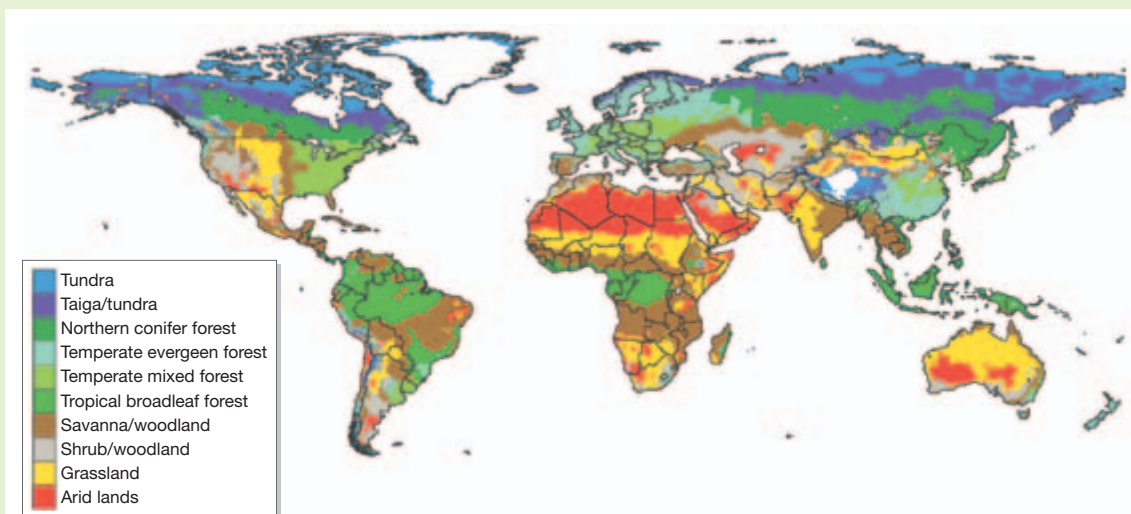
#### Predicted changes in the distribution of biomes as a result of global climate change

As a result of human activities, the atmosphere contains increasing concentrations of certain gases, particularly carbon dioxide, but also nitrous oxide, methane, ozone and chlorofluorocarbons (CFCs). These changes are predicted to lead to increased temperatures and altered patterns of climate over the face of the Earth (see Section 13.3.1). Given the controlling influence of climate on the distribution of biomes, ecologists expect the biome map of the world to change significantly as carbon dioxide concentrations double over the next 60–70 years.

It is no easy matter to predict the precise details of future climate or its consequences for biome distribution. Scientists have come up with a number of feasible scenarios, which differ according to the basic assumptions included in their models. The details of

these need not concern us here. It is enough to note that the simulations shown in Figures 4.12 and 4.13 are based on a climate change model that assumes an effective doubling of carbon dioxide concentrations and takes into account the coupling of atmosphere and ocean in determining changes in patterns of temperature and rainfall. The model is known as MAPSS. This is translated into patterns in the distribution of biomes by simulating the potential mature vegetation that could live under the 'average' seasonal climate prevailing (see Neilson et al., 1998, for further details).

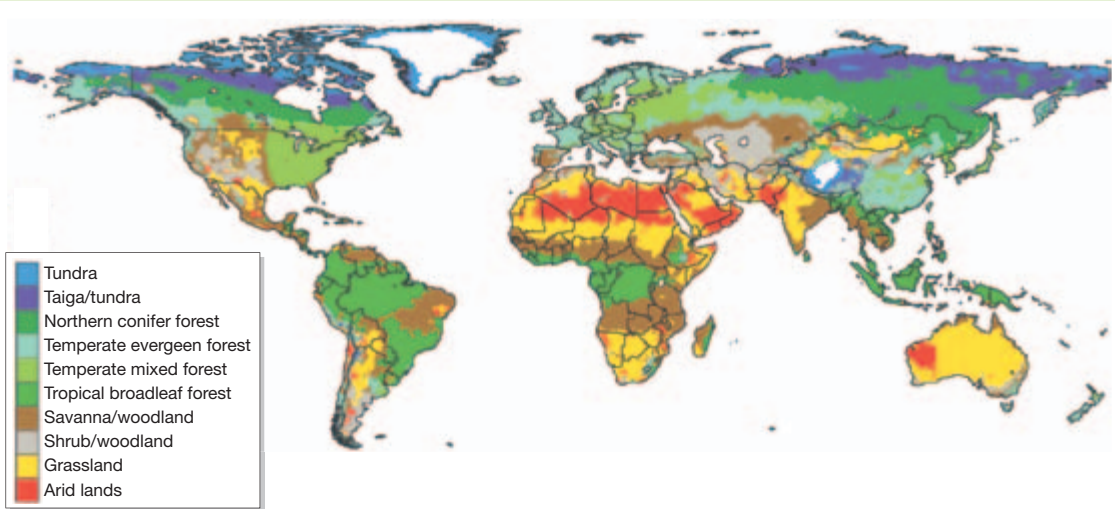
The distribution of biomes shown in Figure 4.12 is as simulated by the model for current climate conditions (Neilson et al., 1998). In other words, it is the model's picture of the way biomes are distributed now (and reflects reality well; note that the biome



**Figure 4.12**

The distribution of major biome types under the current climate, as simulated by the MAPSS biogeography model.

AFTER NEILSON ET AL., 1998



**Figure 4.13**

The potential distribution of major biomes resulting from climate changes associated with an effective doubling of carbon dioxide concentration, as simulated by the MAPSS biogeography model.

AFTER NEILSON ET AL., 1998

categories are not exactly the same as those we discuss elsewhere in the chapter). The map in Figure 4.13, by contrast, is the predicted distribution of biomes in 60–70 years' time (Neilson et al., 1998). This model predicts a reduction in area of the northern biomes of tundra and taiga/tundra (the open woodland that

occurs between the treeless taiga and the dense northern coniferous forest). It also predicts a decrease in arid lands and an increase in temperate forest. These conclusions are in broad agreement with a variety of models that incorporate different starting assumptions.

## 4.5 Aquatic environments

The dominating characteristics of aquatic environments result from the physical properties of water. A water molecule is composed of an oxygen atom, which is slightly negatively charged, bonded with two hydrogen atoms, which are slightly positively charged. This dipolar structure enables water molecules to attract and dissolve more substances than any other liquid on Earth. Consequently, water can hold mineral ions in solution, providing the nutrient resources required for the growth of algae and higher plants.

On the other hand, the solubility of oxygen, an essential resource for both plants and animals, decreases rapidly with increasing temperature, and oxygen diffuses only slowly in water. This problem can place major limits on life in water. Oxygen is rapidly used up when dead organic matter decomposes. In places where tree leaves accumulate or untreated sewage is discharged into a river or lake, decomposition can create anaerobic conditions, which are lethal for fish and other

the special properties of water as  
a medium in which to live



animals that have a high biological oxygen demand. Many aquatic animals maintain access to oxygen by forcing a continual flow of water over their respiratory surfaces (e.g. the gills of fish) or have very large surface areas relative to their body volume.

Water is viscous, and moving water transports whole living organisms, such as small plants and animals. It offers resistance to the movement of motile animals such as fish, otters and aquatic birds; not surprisingly, many motile aquatic animals are streamlined. Many plants that live in moving water depend on rooting in the substratum to hold them against water currents, and many smaller animals are attached to the plants or hide in crevices or under rocks where they are protected from the drag of moving water.

Water is unusual in remaining liquid over a wide range of temperatures. It requires a lot of energy to heat it (i.e. it has high thermal capacity), but retains heat efficiently. One consequence is that the temperature of large bodies of water (oceans and large lakes) varies little over the seasons. A further peculiar physical property of water is that it is less dense when frozen than when liquid. Like most liquids, water becomes denser and sinks as it cools. However, at temperatures below 4°C, water becomes less dense and when ice forms (at 0°C), it floats. Ice on a water surface insulates the water beneath; lakes and streams can remain liquid, free-flowing and inhabitable under a layer of ice.

### 4.5.1 Stream ecology

Streams and rivers contain a minute portion of the world's water (0.006%), but an enormous proportion of the fresh water that can be used by people. Consequently, they have been tapped, dammed, straightened, rerouted, dredged and polluted since the beginning of civilization. Understanding the impacts and sustainability of some of these practices begins with understanding the basics of stream ecology.

Streams and rivers are characterized by their linear form, unidirectional flow, fluctuating discharge and unstable beds. The narrow nature of river channels means that they are very intimately connected to the surrounding terrestrial environment. Thus, a proper understanding of river ecology requires us to consider the river and its drainage basin as a unit (see Section 1.3.3).

Oxygen concentration is often high in turbulent, upstream locations and low farther downstream, where higher temperatures cause reduced solubility. This is reflected in river fish communities, with active upstream species such as brown trout (*Salmo trutta*) having a high oxygen demand, whereas more sluggish species such as pike (*Esox lucius*) can tolerate the lower concentrations in their habitats downstream.

A variety of other chemical and physical conditions vary from stream to stream, or down the length of a given river. Figure 4.14 illustrates how the species composition of stream invertebrate communities varies with conditions. There were 30–40 species at each site (mainly the larvae of stoneflies, caddisflies and chironomid midges) with much overlap in the list of species present. The data were subjected to an analysis called *community classification*, which is conceptually similar to taxonomic classification. In taxonomy, similar individuals are grouped together in species, similar species in genera, and so on. In community classification, communities with similar species compositions are grouped together in

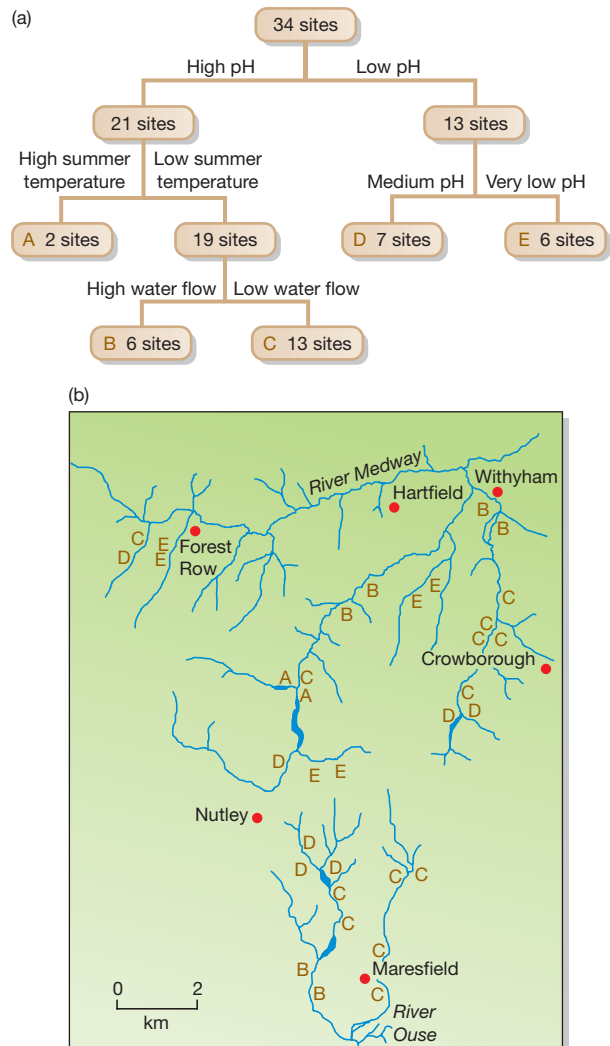
the importance of oxygen  
concentration, ...

... pH and temperature ...

**Figure 4.14**

The species composition of stream invertebrate communities varies with conditions such as pH, summer temperature and waterflow.

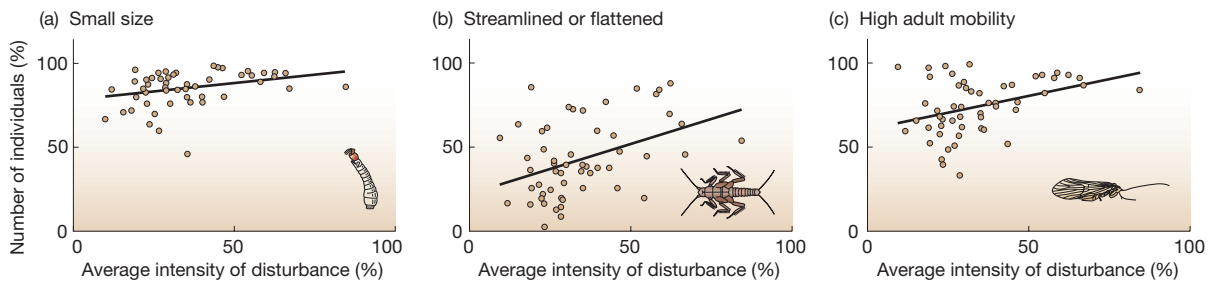
(a) Classification of 34 stream communities. At each division, the communities are divided into classes with similar species compositions, and these divisions can be linked to particular differences in conditions, as shown. The classes are identified by the letters A–E. (b) The actual geographic distribution of community classes A–E in southern England. The classes associated with acid water conditions (D, E) occur typically in the headwaters of the streams.



sets. These sets are then, in turn, grouped into more inclusive sets, and so on. In this case, the conditions that were most influential in determining the pattern of grouping – and thus were most influential in determining community composition – were pH, stream temperature and the volume of water flowing per unit time (discharge).

Because stream discharge responds to events such as thunderstorms and snowmelt, streams are highly disturbed systems. Stream ecologists have recently been looking at ways in which different regimes of disturbance of the streambed are reflected in the composition of the community. For example, the disturbance regimes of 54 stream sites in New Zealand were assessed by painting particles (pebbles, cobbles, boulders) representative of the streambeds and determining the percentage that moved during several periods; this varied from 10% to 85%. The insect inhabitants of the streams were categorized according to properties that might help them deal with highly disturbed conditions, including small size

... and disturbance of the streambed



**Figure 4.15**

Disturbance plays an important role in stream ecology, particularly of stream insects. Disturbed streams contained proportionately more larval insects that (a) were small, (b) had streamlined bodies, and (c) became adults that were strong fliers: characteristics that would enable these insects to withstand a disturbance and recolonize afterward. The best-fit lines (see Box 1.2) are very highly significant in every case ( $P < 0.001$ ).

(small species generally have short life cycles and their populations can rapidly rebuild), a streamlined or flattened body (less prone to being dislodged) and good powers of flight of the adult insects that emerge from the stream to mate (more likely to recolonize after a disturbance). The representation of these traits was higher in the more disturbed streams, testifying to the ecological importance of disturbance regime (Figure 4.15).

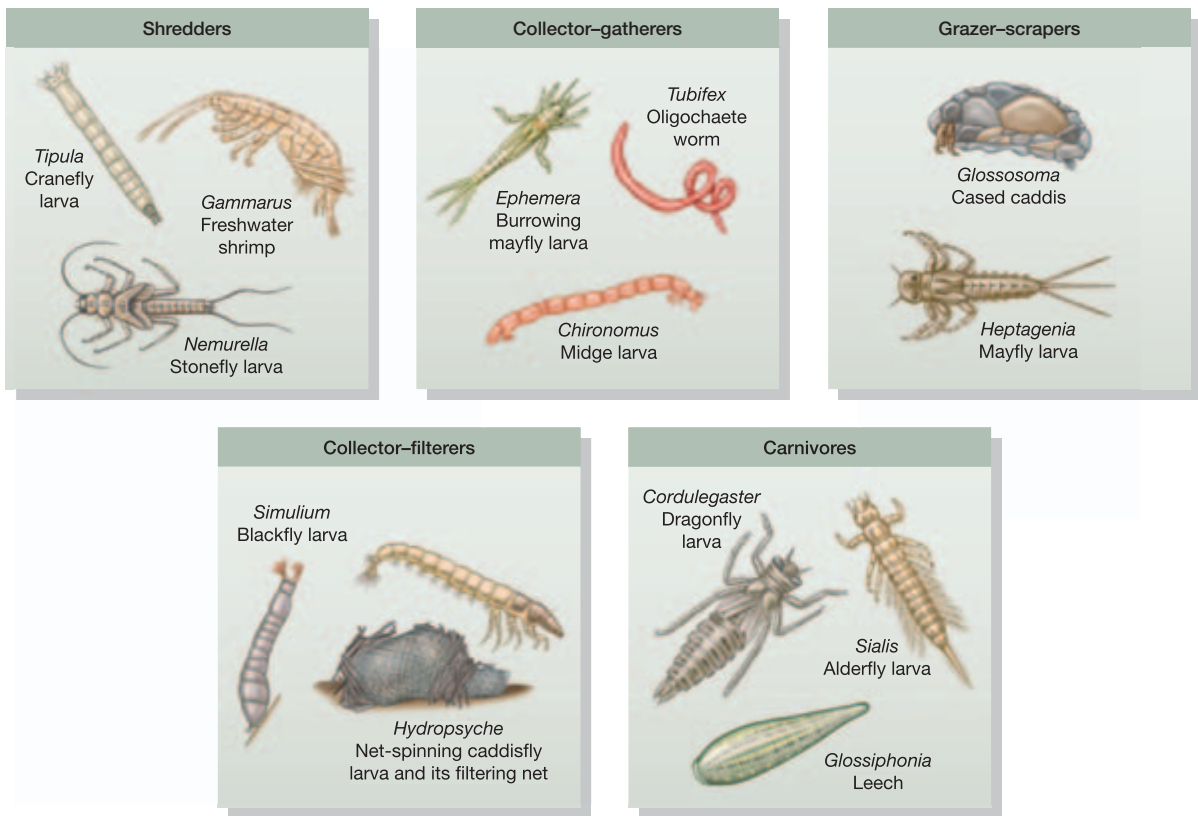
The terrestrial vegetation surrounding a stream (the *riparian* vegetation) has two influences on the resources available to its inhabitants. First, by shading the streambed it may reduce primary production of attached algae and other plants. Second, by shedding leaves it can contribute directly to the food supply of animals and microorganisms. Rivers that begin their course in forested regions are often dominated by the external supply of organic matter, and many of the invertebrates have mouthparts that can handle large particles (*shredders*) (Vannote et al., 1980). Farther downstream, where the stream is wider and where shading is less intense, invertebrates that graze or scrape algae from stones (grazer-scrappers) may be more abundant. As a result of the shredding of large particles into small organic particles (and also physical processes that break up leaves), food for *collector-gatherers* and *collector-filterers* may also increase downstream (Figure 4.16).

When riparian vegetation is changed, for example when forest is converted to agriculture, there can be far-reaching effects. Less particulate organic matter enters the stream, but there is less shading and more nutrient runoff from farmland. Results are an increase in productivity of stream plants and a corresponding change in the stream food web. There may also be effects on discharge (increased when trees are removed), water temperature (higher if shading removed) and streambed characteristics (increased input of fine mineral particles). The more specific consequences of one particular interaction between human activity and stream ecology are described in Box 4.2.

The intimate relationship between land and water is also obvious on the floodplains of rivers such as the Amazon, where seasonal floods inundate huge areas of surrounding forest and provide massive inputs of nutrients and organic matter to the river. Many of the world's floodplains have been deliberately drained or cut off from their associated river channels, with profound consequences for river ecology.

interactions between the stream  
and surrounding land

may be disrupted by human  
activities



**Figure 4.16**

Examples of the various categories of invertebrate consumers in stream environments.



## 4.2 TOPICAL ECOncerns

### A tiny stream fish with big consequences for property development

Because streams are so intimately connected with their terrestrial catchment areas, human activities in their vicinity can have negative consequences for stream ecology. For example, landscaping or the construction of roads and buildings in the vicinity of waterways increases soil erosion and leads to silt runoff into streams. The Cherokee darter (*Etheostoma scotti*) lives in clear streams with beds made up of pebbles and cobbles. Streambeds covered in silt deny this species the ability to forage and spawn; it is now restricted to just a few streams.



COURTESY OF GEORGIA MUSEUM OF NATURAL HISTORY, E. SCOTTI\_RICHLAND CREEK BJF0211

The following article by Clint Williams appeared in the *Atlanta Journal* on July 2, 2001.

#### Cherokee darter: tiny fish forces changes to project

While barely 2 inches long, the Cherokee darter has the power to move roads and redesign a golf course.

The tiny fish, protected under the federal Endangered Species Act, swims in the small, gravel-bottomed streams that wind through a planned 730-acre gated community straddling the Cobb-Paulding county line. And it's forcing the developer to reshape his plans in order to protect the fish.

'We have fine-tuned our layout in order to minimize our impact on the Cherokee darter', said Joe Horton, developer of the Governor's Club, a high-dollar golf course development. 'We're now on our sixth-generation site plan', Horton said.

The Cherokee darter, pale straw yellow with dark olive markings, was listed as threatened by the US Fish and Wildlife Service in 1994, not long after it was identified as a species distinct from the Coosa darter. The Cherokee darter is found only in roughly 20 small tributary systems of the Etowah River, according to a Fish and Wildlife report. But just a few streams have healthy populations.

'It's in a number of streams but that number is declining rapidly', said Seth Winger, a conservation ecologist at the Institute of Ecology at the University of Georgia.

The creeks running through the Governor's Club property are tributaries of Pumpkinvine Creek, which flows into the Etowah River below Allatoona Dam. There are 8000 feet of creeks on the tract, Horton said. A biological survey conducted before purchasing the property found four Cherokee darters . . . 'We're proud we have them', Horton said.

Having them will be a bit costly, however.

(Reproduced by permission of the PARS International Corp.)

- 1 *Is it reasonable that a small population of a species that occurs in about 20 other streams should disrupt economic development?*
- 2 *More specifically, how widespread would the species have to be (in how many streams, in how many states or countries) before developers should be allowed to ignore it?*
- 3 *Do you think it should be the responsibility of ecologists, such as the one quoted, simply to inform the public of the facts (as in this article)? Or is it reasonable for them to become involved in advocacy for a conservation cause?*

### 4.5.2 Lake ecology

Just as river ecology is defined by the unidirectional flow of water, lake ecology is defined by the relatively stationary nature of water within its basin. A critical component of lake ecology is the way in which water can stratify vertically in response to temperature (as mentioned in Section 4.2.3). As water sits in a lake basin, the upper layer is exposed to the sun and heats up. Because warm water is less dense than cold (and therefore tends to rise) the top layer stratifies – that is to say, it forms a layer that is quite separate from the colder water beneath. This layer, the *epilimnion*, is warm and well illuminated and has high oxygen content because surface waters exchange oxygen with the atmosphere. It is usually extremely productive, with high densities of plant and animal life.

In deeper lakes two further layers may form. Below the epilimnion is a transitional layer, the *thermocline*, in which temperature, oxygen concentration and light all decrease. The deepest layer, the *hypolimnion*, is cold and often poor in oxygen.

lakes may become thermally stratified, with major consequences for their ecology

It is here that sunken dead organic matter is decomposed and its mineral nutrients released. In temperate regions of the Earth, stratification of lake water breaks down in the fall when the upper layer cools. Currents then mix the water layers and the minerals released in the hypolimnion become available at the lake surface.

Lake ecologists are increasingly turning their attention to the larger spatial scale of whole lake districts. Lakes high in a landscape (such as those in northern Wisconsin) receive a greater proportion of their water from direct precipitation, whereas lakes at lower altitudes receive more water as an input from ground water (Figure 4.17). This is reflected in the higher concentrations of important ions in lakes low in the landscape. The contrasting ion concentrations can be expected, for example, to affect the ecology and distribution of freshwater sponges, whose skeletons require silica, and crayfish and snails, which have a particular need for calcium.

Nutrient-rich lakes may support a rich flora of microscopic, floating phytoplankton (microscopic plants), together with a diversity of invertebrates and fish species, but a rooted flora of flowering plants is confined to shallow waters near the shore, the *littoral zone*. This zone is usually rich in oxygen, light, food resources and hiding places. However, some fish and invertebrates specialize in the deeper colder waters of lakes. Lake trout (*Salvelinus namaycush*) and walleye (*Sander vitreus*) are two popular sport fish whose habitat is restricted to the colder regions of lakes.

saline lakes are common in some parts of the world

Many lakes in arid regions, lacking a stream outflow, lose water only by evaporation and become rich in sodium and other ions. These saline lakes should not be considered as oddities; globally, they are just as abundant as freshwater lakes. They are usually very fertile and have dense populations of blue-green algae, and some, such as Lake Nakuru in Kenya, support huge aggregations of plankton-filtering flamingoes (*Phoenicopterus roseus*).

### 4.5.3 The oceans

The oceans cover the major part of the Earth's surface and receive most of the Earth's income of solar radiation. However, much of this radiation is reflected at the water surface or absorbed by water itself and by particles in suspension. Even in clear water the intensity of radiation falls off exponentially with depth and photosynthesis is mainly restricted to the upper 100 m – the *euphotic zone*. In most waters the euphotic zone is much shallower, especially where water is more turbid close to coasts and estuaries.

The green plants that photosynthesize in the open oceans are planktonic, mainly single-celled algae that are capable of using solar radiation very efficiently. But, in the real world, many areas of ocean that receive the greatest intensity of solar radiation have the lowest biological activity – because plant productivity is limited by shortage of mineral nutrients. The great tropical parts of the Atlantic and Pacific Oceans have a biological productivity of less than 35 g carbon (g C) m<sup>-2</sup> yr<sup>-1</sup>. This compares with more than 800 g C m<sup>-2</sup> yr<sup>-1</sup> in terrestrial communities at the same latitudes.

The areas of greatest marine productivity (exceeding 90 g C m<sup>-2</sup> yr<sup>-1</sup>) occur where there is a reliable supply of minerals (especially nitrogen and phosphorus, and perhaps iron). This occurs via leaching from the land through rivers and estuaries or where deep currents in the oceans well up to the surface and bring dissolved



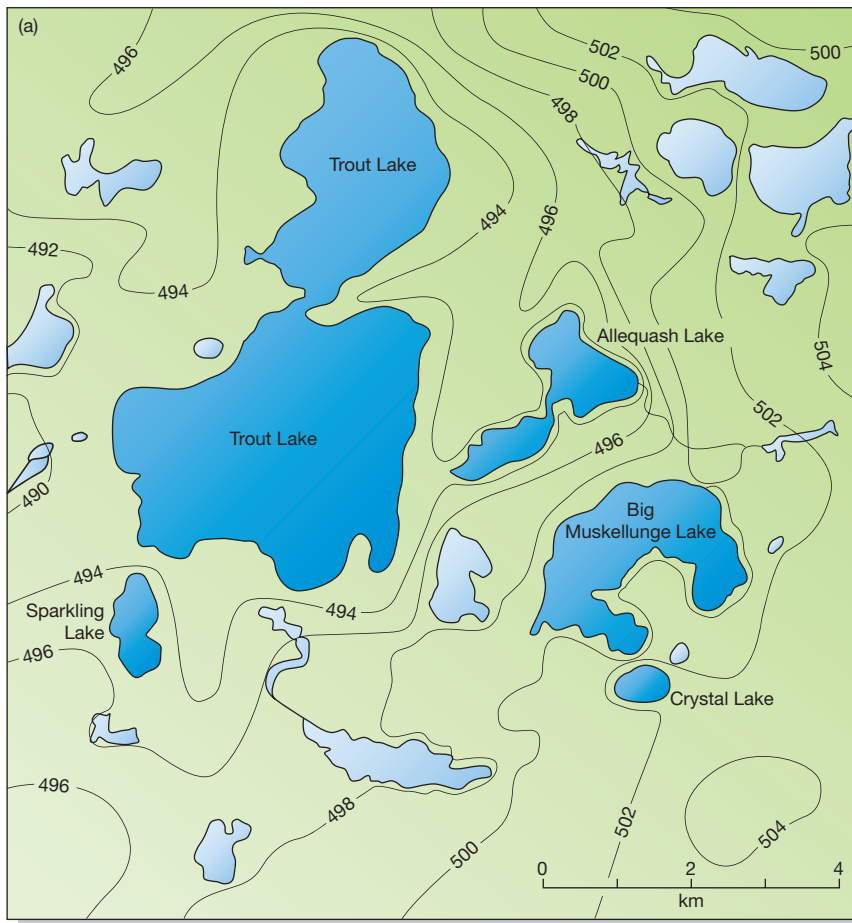
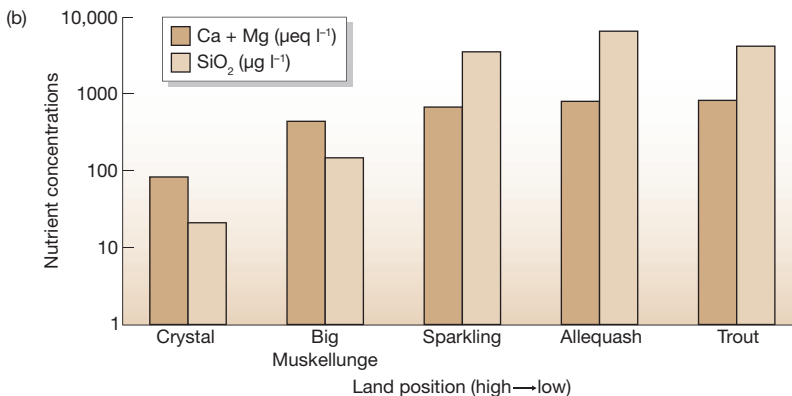


Figure 4.17

Lakes at different positions in the landscape differ in the source of their water and the concentrations of chemicals important to their inhabitants. (a) Map of Wisconsin Lake District: study lakes are darkly shaded and contours are shown (meters above sea level). (b) Relationships between landscape position and concentrations of calcium and magnesium ( $\text{Ca} + \text{Mg}$ ) and silica ( $\text{SiO}_2$ ) in the five lakes. Lakes higher in the catchment area (Crystal and Big Muskellunge) have lower nutrient concentrations.



nutrients into the euphotic zone (see Section 11.2.2). In areas where upwellings occur, the ocean 'desert' becomes transformed to a productive environment, as, for example, off the coast of Peru. Dense populations of planktonic algae support small crustacea, which in turn are eaten by schools of anchovies (*Engraulis ringens*). The fish support sea lions, and flocks of cormorants, pelicans and gannets.

unique communities occur in the abyssal depths of the oceans

We saw earlier in this chapter that the distribution of terrestrial communities depends largely on the intensity of solar radiation and its effects on temperature and water availability. In complete contrast, variations between oceanic communities are ruled mainly by the availability of mineral nutrients.

Below the euphotic zone is increasing darkness, and the ocean floor is in total darkness, intensely cold and under great pressure. This abyssal environment supports the very slow biological activity of a community of extraordinary biological diversity (including worms, crustaceans, mollusks and fish found nowhere else), which depends on the rain of dying and dead organisms falling from the euphotic zone above. Many of the invertebrate animals are tiny, have very low metabolic rates and possess a lifespan that may last for decades. Yet further diversity occurs in hydrothermal vents that occur at a number of isolated places 2000–4000 m deep (see Box 2.2). In these remarkable environments, there are high sulfide concentrations and very high temperatures, up to 350°C, where superheated fluid emerges from ‘chimneys’, and there is a sharp gradient down to 2°C, the temperature normally encountered in abyssal depths close by. The vent areas are inhabited by productive thermophilic (heat-loving) bacteria and a unique fauna of polychaete worms, crabs and very large mollusks.

#### 4.5.4 Coasts

Marine environments change dramatically near to coasts. Not only are they enriched by nutrients from the land; they are also affected by waves and tides that bring new physical forces to bear. In particular, there are now surfaces to which organisms can attach; indeed, if they do not do so they are liable to be washed out to sea or stranded on the shore. At a broad scale, coastal communities are strongly influenced by waves and tides and the topography of the coast. Within a single stretch of coast, we can recognize a zonation in the flora and fauna marked by high and low tide levels (Figure 4.18). Such zonation patterns are more obvious in sheltered situations where wave action is light, but become more fuzzy in very exposed situations.

waves and tides are key influences in coastal ecology

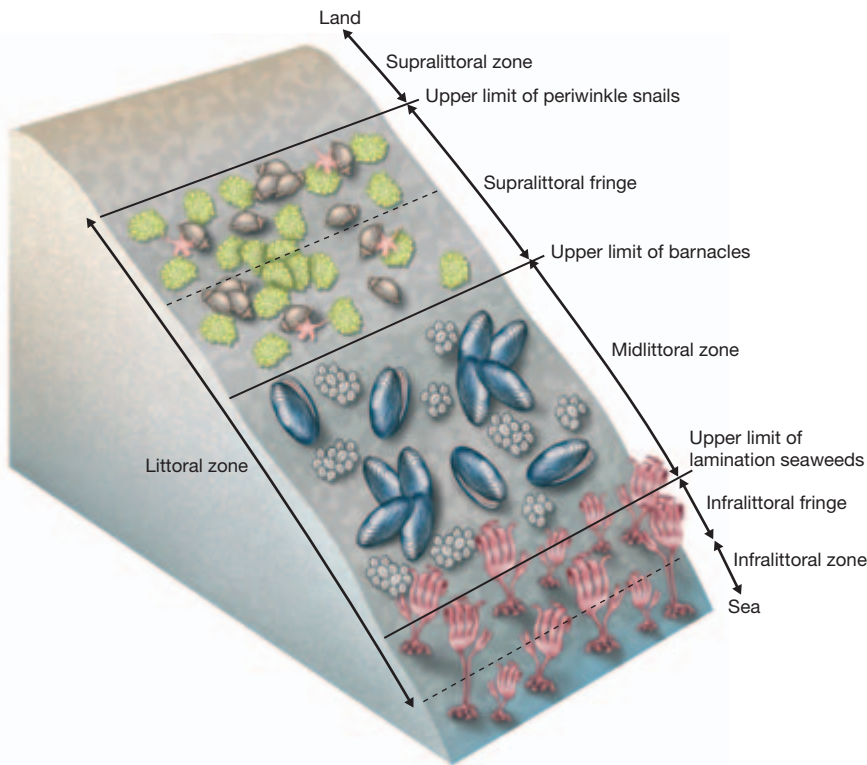
The extent of the littoral zone depends on the height of tides and the slope of the shore. Away from the shore, the tidal rise and fall are rarely greater than 1 m, but closer to shore, the shape of the land mass can funnel the ebb and flow of the water to produce extraordinary spring tidal ranges of, for example, nearly 20 m in the Bay of Fundy (between Nova Scotia and New Brunswick, Canada). In contrast, the shores of the Mediterranean Sea experience scarcely any tidal range.

On steep shores and rocky cliffs the littoral zone is very narrow and zonation is compressed. Both plants and animals are profoundly affected by the physical force of wave action. Anemones, barnacles and mussels attach themselves securely and permanently to the substrate and filter planktonic plants and animals from the water when the tides cover them. Other animals, such as limpets, move to graze, and crabs move with the tides and use rock crevices as refuges. The flora in a rocky infralittoral zone (Figure 4.18) is usually dominated by the large brown seaweeds (kelps), which fix themselves to the rock with specialized ‘holdfasts’.

Environments are quite different on shallow sloping shores on which the tides deposit and stir up sand and mud. Here the dominant animals are mollusks

Figure 4.18

A general zonation scheme for the seashore determined by relative lengths of exposure to the air and to the action of waves. At the top of the shore is the supralittoral zone (the splash zone above the high tide level). The littoral zone, between high and low tide levels, can be divided into a midlittoral zone together with a supralittoral fringe above and an infralittoral fringe below. The infralittoral zone proper lies below the low tidal limit. Characteristic communities of animals and plants occur in these different zonation bands.



AFTER RAFFAELLI & HAWKINS, 1996

and polychaete worms, living buried in the substrate and feeding by filtering the water when they are covered by the tides. This environment is completely free of large seaweeds, whose holdfasts can find no anchorage. Flowering plants are almost, but not completely, absent from intertidal environments. The exceptions occur where it is possible for them to be anchored by their roots and this requirement limits them to the more stable and muddy areas colonized by 'sea grasses' such as *Zostera* and *Posidonia* or tussocks of *Spartina*. In the tropics, mangroves occupy this kind of habitat, adding a shrubby, woody dimension to the marine littoral zone.

#### 4.5.5 Estuaries

Estuaries occur at the confluence of a river (fresh water) and a tidal bay (salt water). They provide an intriguing mix of the conditions normally experienced in rivers, shallow lakes and tidal communities. Salt water, more dense than fresh water, tends to enter along the bottom of an estuary as a salt wedge. As it mixes with the outflowing fresh water, a brackish middle layer is created, then it returns downstream on the outgoing tide. The shape of the saltwater wedge is largely determined by the size of the discharge of the river flowing into the estuary; high discharge tends to create a smaller wedge of salt water and less mixing. The strong gradients in salinity, in both space and time, are reflected in a specialized estuarine fauna. Some animals cope through particular physiological mechanisms. Others avoid the variable salt concentrations by burrowing, closing protective shells or moving away when conditions do not favor them.



## Summary

# SUMMARY

### Geographic patterns at large and small scales

The variety of influences on climatic conditions over the surface of the globe causes a mosaic of climates. This, in turn, is responsible for the large-scale pattern of distribution of terrestrial biomes. However, biomes are not homogeneous within their hypothetical boundaries; every biome has gradients of physicochemical conditions related to local topographic, geological and soil features. The communities of plants and animals that occur in these different locations may be quite distinct.

In most aquatic environments it is difficult to recognize anything comparable to terrestrial biomes; the communities of streams, rivers, lakes, estuaries and open oceans reflect local conditions and resources rather than global patterns in climate. The composition of local communities can change over time scales ranging from hours, through decades, to millennia.

### Terrestrial biomes

A map of biomes is not usually a map of the distribution of species. Instead, it shows where we find areas of land dominated by plants with characteristic life forms.

Tropical rain forest represents the global peak of evolved biological diversity. Its exceptional productivity results from the coincidence of high solar radiation received throughout the year and regular and reliable rainfall.

Savanna consists of grassland with scattered small trees. Seasonal rainfall places the most severe restrictions on the diversity of plants and animals in savanna; grazing herbivores and fire also influence the vegetation, favoring grasses and hindering the regeneration of trees.

Temperate grassland occurs in the steppes, prairies and pampas. Typically, it experiences seasonal drought, but the role of climate in determining vegetation is usually overridden by the effects of grazing animals. Humans have transformed temperate grassland more than any other biome.

Many desert plants have an opportunistic lifestyle, stimulated into germination by the unpredictable rains; others, such as cacti, are long-lived and have sluggish physiological processes. Animal diversity is low in deserts, reflecting the low productivity of the vegetation and the indigestibility of much of it.

Temperate forests at lower latitudes experience mild winters, and the vegetation consists of broad-leaved, evergreen trees. Nearer the poles, the seasons are strongly marked, and vegetation is dominated by deciduous trees. Soils are usually rich in organic matter.

Northern coniferous forests have few tree species and contrast strongly with the biodiversity of tropical rain forests, reflecting a slow recovery from the catastrophes of the ice ages, and the overriding local constraint of frozen soil. Nearer the poles, the vegetation changes to tundra, and the two often form a mosaic in the Low Arctic. The mammal populations of the northern biomes often pass through remarkable cycles of expansion and collapse.

### Aquatic environments

Streams and rivers are characterized by their linear form, unidirectional flow, fluctuating discharge and unstable beds. The terrestrial vegetation surrounding a stream has strong influences on the resources available to its inhabitants; the conversion of forest to agriculture can have far-reaching effects.

Lake ecology is defined by the relatively stationary nature of its water. Some lakes stratify vertically in response to temperature, with consequences for the availability of oxygen and plant nutrients. Lakes higher in a landscape may receive more of their water from rainfall; those at lower altitude receive more from ground water. Saline lakes in arid regions lack a stream outflow and lose water only by evaporation.

The oceans cover the major part of the Earth's surface and receive most of the solar radiation. However, many areas have very low biological activity

because of a shortage of mineral nutrients. Below the surface zone is increasing darkness, but at the ocean floor there may be an abyssal environment that supports a diverse community with very slow biological activity.

Coastal communities are enriched by nutrients from the land, but they are also affected by waves

and tides. Within a single stretch of coast, there is a zonation in the flora and fauna that differs between areas with heavy or light wave action.

Estuaries occur at the confluence of a river (fresh water) and a tidal bay (salt water). Strong gradients in salinity, in both space and time, are reflected in a specialized estuarine fauna.

## *Review questions*

### REVIEW QUESTIONS

Asterisks indicate challenge questions

- 1 Describe the various changes in climate that occur with changing latitude, including an explanation of why deserts are more likely to be found at around 30° latitude than at other latitudes.
- 2 How would you expect the climate to change as you crossed from west to east over the Rocky Mountains?
- 3\* Biomes are differentiated by gross differences in the nature of their communities, not by the species that happen to be present. Explain why this is so.
- 4 The tropical rain forest is a diverse community supported by a nutrient-poor soil. Account for this.
- 5\* Which of the Earth's biomes do you think have been most strongly influenced by people? How and why have some biomes been more strongly affected by human activity than others?
- 6 What is meant by the 'stratification' of water in lakes? How does it occur? And what are the reasons for variations in stratification from time to time and from lake to lake?
- 7 Describe how the logging of a forest may influence the community of organisms inhabiting a stream running through the affected area.
- 8 Why is much of the open ocean, in effect, a 'marine desert'?
- 9 Discuss some reasons why community composition changes as one moves (i) up a mountain, and (ii) down the continental shelf into the abyssal depths of the ocean.
- 10\* Why are broad geographic classifications of aquatic communities less feasible than broad geographic classifications of terrestrial communities? What characteristics of aquatic ecosystems buffer the effects of climate?







# PART THREE

## Individuals, Populations, Communities and Ecosystems

- 5 | Birth, death and movement 145
- 6 | Interspecific competition 182
- 7 | Predation, grazing and disease 217
- 8 | Evolutionary ecology 251
- 9 | From populations to communities 281
- 10 | Patterns in species richness 323
- 11 | The flux of energy and matter through ecosystems 357



# Chapter 5



## Birth, death and movement

### *Chapter contents*

#### CHAPTER CONTENTS

- 5.1 Introduction
- 5.2 Life cycles
- 5.3 Monitoring birth and death: life tables and fecundity schedules
- 5.4 Dispersal and migration
- 5.5 The impact of intraspecific competition on populations
- 5.6 Life history patterns

### *Key concepts*

#### KEY CONCEPTS

In this chapter you will:

- appreciate the difficulties of counting individuals, but the necessity of doing so for understanding the distribution and abundance of organisms and populations
- appreciate the range of life cycles and patterns of birth and death exhibited by different organisms
- understand the nature and the importance of life tables and fecundity schedules
- understand the role and the importance of dispersal and migration in the dynamics of populations
- understand the impact of intraspecific competition on birth, death and movement, and hence on populations
- appreciate that life history patterns linking types of organism to types of habitat can be constructed but also recognize the limitations of those patterns

*All questions in ecology – however scientifically fundamental, however crucial to immediate human needs and aspirations – can be reduced to attempts to understand the distributions and abundances of organisms, and the processes – birth, death and movement – that determine distribution and abundance.*

*In this chapter, these processes, the methods of monitoring them and their consequences are introduced.*

## 5.1 Introduction

what is a population?

As ecologists, we try to describe and understand the distribution and abundance of organisms. We may do so because we wish to control a pest or conserve an endangered species, or simply because we are fascinated by the world around us and the forces that govern it. A major part of our task, therefore, involves studying changes in the size of populations. We use the term *population* to describe a group of individuals of one species. What actually constitutes a population, though, varies from species to species and from study to study. In some cases, the boundaries of a population are obvious: the sticklebacks occupying a small lake are ‘the stickleback population of the lake’. In other cases, boundaries are determined more by an investigator’s purpose or convenience. Thus, we may study the population of lime aphids inhabiting one leaf, one tree, one stand of trees or a whole woodland. What is common to all uses of *population* is that it is defined by the number of individuals that compose it: populations grow or decline by changes in those numbers.

birth, death and movement  
change the size of populations

The processes that change the size of populations are birth, death and movement into and out of that population. Trying to understand the causes of changes in population size is important because the science of ecology is not just about understanding nature but often also about predicting or controlling it. We might, for example, wish to reduce the size of a population of rabbits that can do serious harm to crops. We might do this by increasing the death rate by introducing the myxomatosis virus to the population, or by decreasing the birth rate by offering them food that contains a contraceptive. We might encourage their emigration by bringing in dogs, or prevent their immigration by fencing.

Similarly, a nature conservationist may wish to increase the population of a rare endangered species. In the 1970s, the numbers of bald eagles, ospreys and other birds of prey in the United States began a rapid decline. This might have been because their birth rate had fallen, or their death rate had risen, or because the populations were normally maintained by immigration and this had fallen, or because individuals had emigrated and settled elsewhere. Eventually the decline was traced to reduced birth rates. The insecticide DDT (dichlorodiphenyltrichloroethane) was widely used at the time (it is now banned in the United States) and had been absorbed by many species on which the birds preyed. As a result, it accumulated in the bodies of the birds themselves and affected their physiological processes so that the shells of their eggs became so thin

that the chicks often died in the egg. Conservationists charged with restoring the bald eagle population had to find a way to increase the birds' birth rate. The banning of DDT achieved this end.

### 5.1.1 What is an individual?

A population is characterized by the number of individuals it contains, but for some kinds of organism it is not always clear what we mean by an individual. Often there is no problem, especially for *unitary* organisms. Birds, insects, reptiles and mammals are all unitary organisms. The whole form of such organisms, and their program of development from the moment when a sperm fuses with an egg, is predictable and *determinate*. An individual spider has eight legs. A spider that lived a long life would not grow more legs.

But none of this is so simple for *modular* organisms such as trees, shrubs and herbs, corals, sponges and very many other marine invertebrates. These grow by the repeated production of modules (leaves, coral polyps, etc.) and almost always form a branching structure. Such organisms have an architecture: most are rooted or fixed, not motile (Figure 5.1). Both their structure and their precise program of development are not predictable but *indeterminate*. We could count the individual trees in a forest, but would this signify the 'size' of the tree population? Not unless we also noted whether the trees were young saplings (few leaves and branches each), or old individuals, each with many more such modules. Indeed, it may make more sense not to count the individual trees themselves but the total number of modules instead.

In modular organisms, then, we need to distinguish between the genet – the genetic individual – and the module. The *genet* is the individual that starts life as a single-celled zygote and is considered dead only when all its component modules have died. A *module* starts life as a multicellular outgrowth from another module and proceeds through a life cycle to maturity and death even though the form and development of the whole genet are indeterminate. We usually think of unitary organisms when we write or talk about populations, perhaps because we ourselves are unitary, and there are certainly many more species of unitary than of modular organisms. But modular organisms are not rare exceptions and oddities. Most of the living matter (biomass) on Earth and a large part of that in the sea is of modular organisms: the forests, grasslands, coral reefs and peat-forming mosses.

unitary and modular organisms

modular organisms are themselves populations of modules

### 5.1.2 Counting individuals, births and deaths

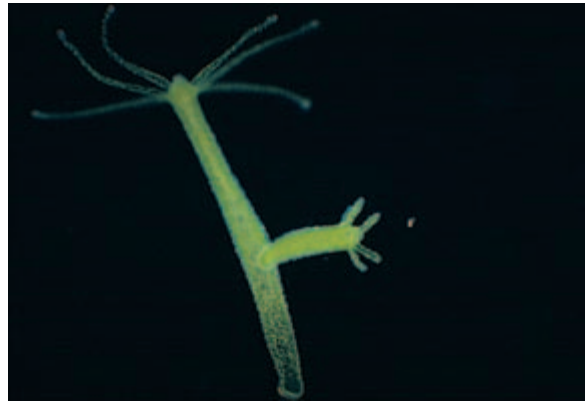
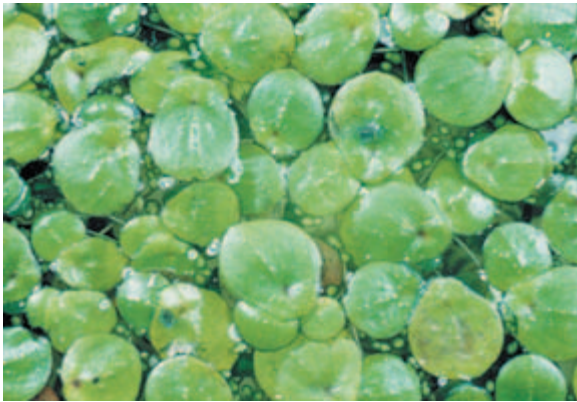
Even with unitary organisms, we face enormous technical problems when we try to count what is happening to populations in nature. A great many ecological questions remain unanswered because of these problems. For example, resources can only be focused on controlling a pest effectively if it is known when its birth rate is highest. But this can only be known by monitoring accurately either births themselves or rising total numbers – neither of which is ever easy.

If we want to know how many fish there are in a pond we might obtain an accurate count by putting in poison and counting the dead bodies. But apart from the questionable morality of doing this, we usually want to continue studying a population after we have counted it. Occasionally it may be possible to trap alive

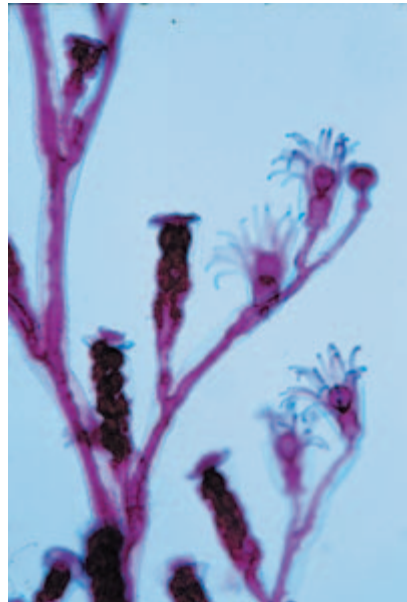
the difficulties of counting



(a)



(b)



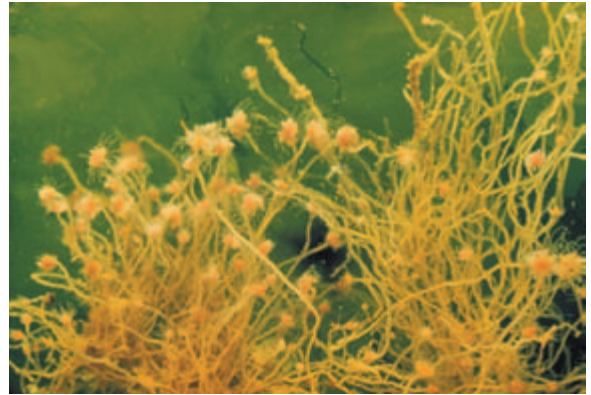
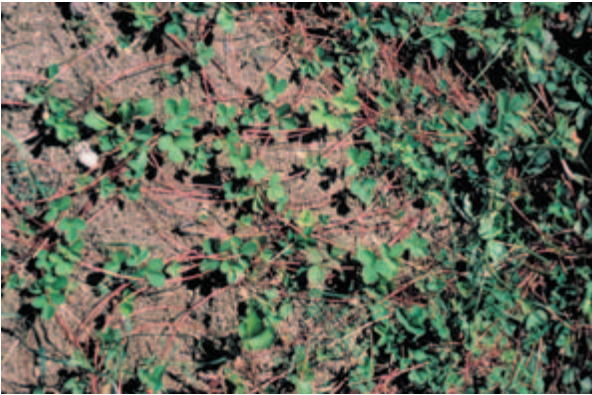
**Figure 5.1**

Modular plants (on the left) and animals (on the right), showing the underlying parallels in the various ways they may be constructed. (a) Modular organisms that fall to pieces as they grow: duckweed (*Lemna* sp.) (© John D. Cunningham) and *Hydra* sp. (© Larry Stepanowicz). (b) Freely branching organisms in which the modules are displayed as individuals on 'stalks': a vegetative shoot of a higher plant (*Lonicera japonica*) with leaves (feeding modules) and a flowering shoot (© Visuals Unlimited), and a hydroid colony (*Obelia*) bearing both feeding and reproductive modules (© Larry Stepanowicz).

all the individuals in a population, count them and then release them. With birds, for example, it may be possible to mark nestlings with leg rings and ultimately recognize every individual (except immigrants) in the population of a small woodland. It is not too difficult to count the numbers of large mammals such as deer on an isolated island. But it is very much more difficult to count the numbers of lemmings in a patch of tundra because they spend a large part of the year (and



(c)



(d)



(e)



**Figure 5.1** (cont.)

(c) Stoloniferous organisms in which colonies spread laterally and remain joined by 'stolons' or rhizomes: a single plant of strawberry (*Fragaria*) spreading by means of stolons (© Science VU) and a colony of the hydroid *Tubularia crocea* (© John D. Cunningham). (d) Tightly packed colonies of modules: a tussock of the spotted saxifrage (*Saxifraga bronchialis*) (© Gerald and Buff Corsi) and a segment of the hard coral *Turbinaria reniformis* (© Dave B. Fleetham). (e) Modules accumulated on a long, persistent, largely dead support: an oak tree (*Quercus robur*) in which the support is mainly the dead woody tissues derived from previous modules (© Silwood Park) and a gorgonian coral in which the support is mainly heavily calcified tissues from earlier modules (© Daniel W. Gotshall).

estimates from representative samples

may reproduce) under thick snow cover. And most other species are so small, or cryptic, or hidden, or fast moving that they are even more difficult to count.

Ecologists, therefore, are almost always forced to estimate rather than count. They may estimate the numbers of aphids on a crop, for example, by counting the number on a representative sample of leaves, then estimating the number of leaves per square meter of ground, and from this estimating the number of aphids per square meter. Sometimes more complex methods are used (Box 5.1), and at other times we may rely on indirect 'indices' of abundance. These can provide



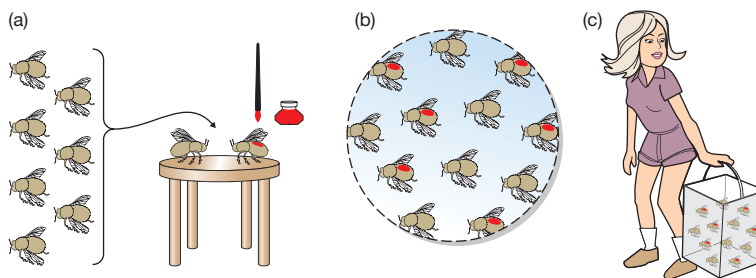
## 5.1 Quantitative aspects

### 5.1 QUANTITATIVE ASPECTS

#### Mark-recapture methods for estimating population size

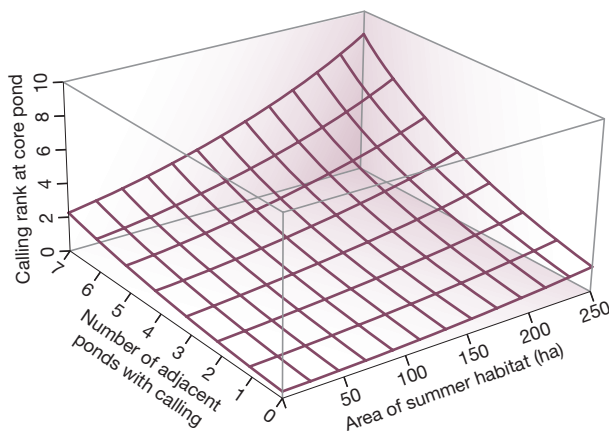
An estimate of the size of a population can sometimes be made by capturing a sample of individuals, marking them in some way (paint spots, leg rings) and then releasing them. Later, another sample is captured, and the proportion that is marked gives some estimate of the size of the whole population (Figure 5.2). For example, we might capture and mark 100 individuals from a population of sparrows and release them back into the population. If we later sample a further 100 individuals from the population and find half are marked, we could argue in the following way: half the sample are marked; the sample is representative of

the whole population; therefore half the population are marked; 100 individuals were given a mark; therefore the whole population is composed of about 200 individuals. But this technique of mark and recapture is far less straightforward than it appears at first sight. There are many pitfalls in the sampling process and in interpretation of the data. Suppose, for example, that many of the individuals we marked died between our first and second visits. Modifications of the method would be needed to take account of this. For many organisms, however, it is the only technique that we have to estimate the size of a population.



**Figure 5.2**

The mark and recapture technique for estimating the size of a population of mobile organisms (in simplified form). (a) On a first visit to a population of unknown total size  $N$ , a representative sample is caught ( $r$  individuals) and given a harmless mark. (b) These are released back into the population, where they remix with the unknown number of unmarked individuals. (c) On a second visit, a further representative sample is caught. Because it is representative, the proportion of marks in the sample ( $m$  out of a total sample of  $n$ ) should, on average, be the same as that in the whole population ( $r$  out of a total of  $N$ ). Hence  $N$  can be estimated.

**Figure 5.3**

The abundance (calling rank) of leopard frogs (*Rana pipiens*) in ponds increases significantly with both the number of adjacent ponds that are occupied and the area of summer habitat within 1 km of the pond. Calling rank is the sum of an index measured on four occasions, namely: 0, no individuals calling; 1, individuals can be counted, calls not overlapping; 2, calls of <15 individuals can be distinguished with some overlapping; 3, calls of  $\geq 15$  individuals.

information on the relative size of a population, but usually give little indication of absolute size. As an example, Figure 5.3 shows how the abundance of Canadian leopard frogs was affected by the number of occupied ponds and the amount of summer (terrestrial) habitat in their vicinity. Here, frog abundance was estimated from the ‘calling rank’: whether there were no frogs, ‘few’, ‘many’ or ‘very many’ frogs calling on each of four occasions. Despite their shortcomings, even indices of abundance can provide valuable information.

Moreover, as we have already noted, for modular organisms it is often not even clear what it is we should be counting.

## 5.2 Life cycles

### 5.2.1 Life cycles and reproduction

If we wish to understand the forces determining the abundance of a population of organisms, we need to know the important phases of those organisms’ lives: that is, the phases when these forces act most significantly. For this, we need to understand the sequences of events that occur in those organisms’ life cycles.

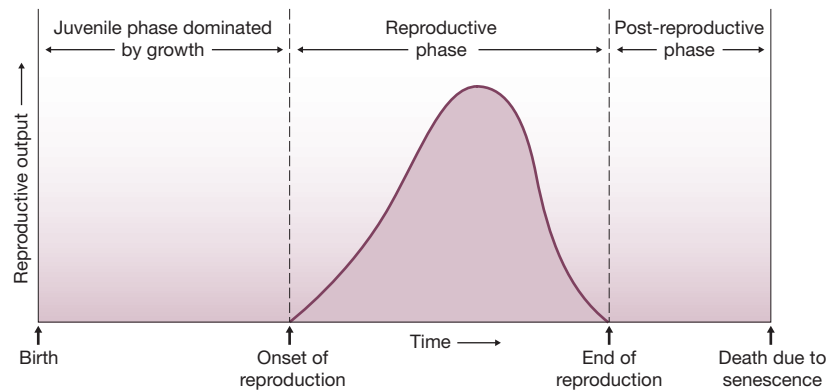
There is a point in the life of any individual when, if it survives that long, it will start to reproduce and leave progeny. A highly simplified, generalized life history (Figure 5.4) comprises birth, followed by a pre-reproductive period, a period of reproduction, a post-reproductive period and then death as a result of senescence (though of course other forms of mortality may intervene at any time). The life histories of all unitary organisms can be seen as variations around this simple pattern, though a post-reproductive period (as seen in humans) is probably rather unusual.

Some organisms fit several or many generations within a single year, some have just one generation each year (annuals) and others (perennials) have a life cycle extended over several or many years. For all organisms, though, a period of growth occurs before there is any reproduction, and growth usually slows down (and in some cases stops altogether) when reproduction starts. Growth and reproduction both require resources and there is clearly some conflict between them. Thus, as the perennial plant *Sparaxis grandiflora* enters its reproductive

the conflict between growth  
and reproduction

**Figure 5.4**

An outline life history for a unitary organism. Time passes along the horizontal axis, which is divided into different phases. Reproductive output is plotted on the vertical axis.



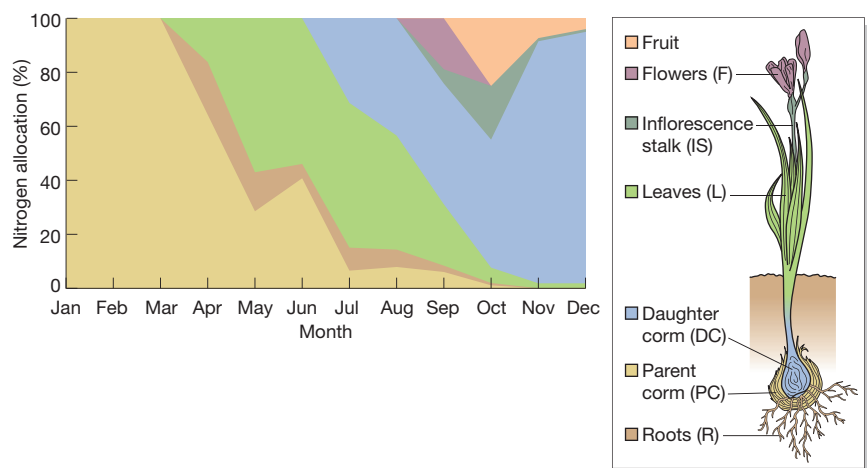
stage in the Southwestern Cape, South Africa, flowers, flower stalks and fruit (aspects of reproduction) can be seen to have been produced *at the expense* of roots and leaves (Figure 5.5). There are also many plants (e.g. foxgloves) that spend their first year in vegetative growth, and then flower and die in the second or a later year (called ‘biennial’ plants). But if the flowers of these species are removed before their seeds begin to set, the plants usually survive to the following year, when they flower again and set seed even more vigorously. It seems to be the cost of provisioning the offspring (seeds) rather than the flowering itself that is lethal. Similarly, pregnant women are advised to increase their caloric intake by as much as half their normal consumption: when nutrition is inadequate, pregnancy can harm the health of the mother.

iteroparous and semelparous species

Among both annuals and perennials, there are some – *iteroparous species* – that breed repeatedly, devoting some of their resources during a breeding episode not to breeding itself, but to survival to further breeding episodes (if they manage to live that long). We ourselves are examples. There are others, *semelparous species*, like the biennial plants already described, in which there is a single reproductive episode, with no resources set aside for future survival, so that reproduction is inevitably followed quickly by death.

**Figure 5.5**

Percentage allocation of the crucial resource nitrogen to different structures throughout the annual cycle of the perennial plant *Sparaxis grandiflora* in South Africa, where it sets fruit in the southern hemisphere spring (September–December). The plant grows each year from a corm, which it replaces over the growing season, but note the development of reproductive parts at the expense of roots and leaves toward the end of the growing season. The plant parts themselves are illustrated to the right for a plant in early spring.





### 5.2.2 Annual life cycles

In strongly seasonal, temperate latitudes, most annuals germinate or hatch as temperatures start to rise in the spring, grow rapidly, reproduce and then die before the end of summer. The European common field grasshopper *Chorthippus brunneus* is an example of an annual species that is iteroparous. It emerges from its egg in late spring and passes through four juvenile stages of nymph before becoming adult in midsummer and dying by mid-November. During their adult life, the females reproduce repeatedly, each time laying egg pods containing about 11 eggs, and recovering and actively maintaining their bodies between the bursts of reproduction.

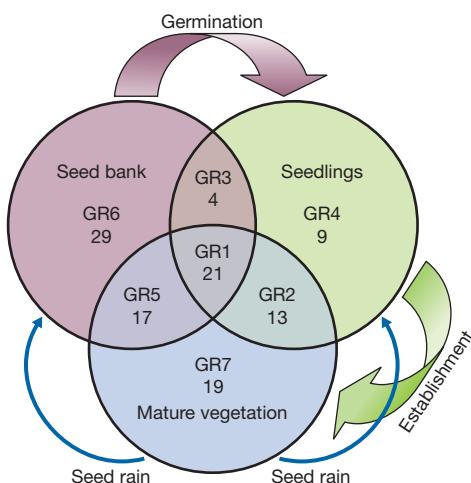
Many annual plants, by contrast, are semelparous: they have a sudden burst of flowering and seed set, and then they die. This is commonly the case among the weeds of arable crops. Others, such as groundsel, are iteroparous: they continue to grow and produce new flowers and seeds through the season until they are killed by the first lethal frost of winter. They die with their buds on.

Most annuals spend part of the year dormant as seeds, spores, cysts or eggs. In many cases these dormant stages may remain viable for many years; there are reliable records of seeds of the annual weeds *Chenopodium album* and *Spergula arvensis* remaining viable in soil for 1600 years. Similarly, the dried eggs of brine shrimps remain viable for many years in storage. This means that if we measure the length of life from the time of formation of the zygote, many so-called ‘annual’ animals and plants live very much longer than a single year. Large populations of dormant seeds form a *seed bank* buried in the soil: as many as 86,000 viable seeds per square meter have been found in cultivated soils. The species composition of the seed bank may be very different from that of the mature vegetation above it (Figure 5.6). Species of annuals that seem to have become locally extinct may suddenly reappear after the soil is disturbed and these seeds germinate.

Dormant seeds, spores or cysts are also necessary to the many ephemeral plants and animals of sand dunes and deserts that complete most of their life cycle in less than 8 weeks. They then depend on the dormant stage to persist through the remainder of the year and survive the hazards of low temperatures in winter and the droughts of summer. In desert environments, in fact, the rare rains are not

seed banks

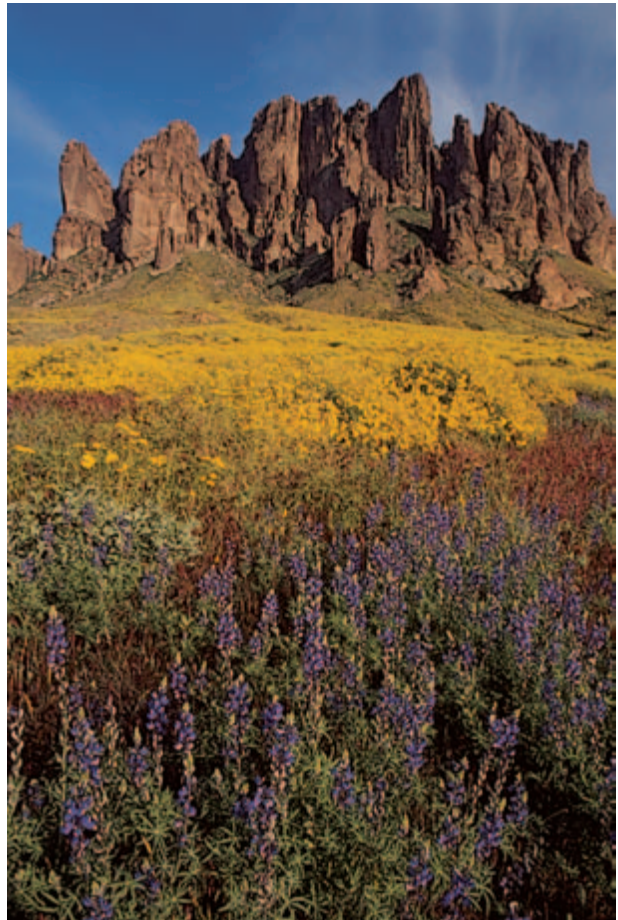
ephemeral ‘annuals’ of deserts



**Figure 5.6**

Species recovered from the seed bank, from seedlings and from the mature vegetation in a coastal grassland site on the western coast of Finland. Species may germinate from the buried seed bank into seedlings, and seedlings may establish themselves in the mature vegetation. Mature plants may contribute seeds (in the ‘seed rain’) that germinate into seedlings immediately or enter the buried seed bank. Seven species groups (GR1–GR7) are defined on the basis of whether they were found in only one, two or all three life stages. The marked difference in composition, especially between the seed bank and the mature vegetation, is readily apparent. Thirty-two species in the mature vegetation (19 + 13) were not represented in the seed bank; 33 species in the seed bank were not found in the mature vegetation, and 29 of these were not found as seedlings either.

A desert in bloom. In desert areas where rainfall is rare and seasonally unpredictable, a dense and spectacular flora of very short-lived annuals commonly develops after rain storms. They often complete their life cycle from germination to seed set in little more than a month.



© DOUG SOXELL, VISUALS UNLIMITED

necessarily seasonal, and it is only in occasional years that sufficient rain falls and stimulates the germination of characteristic and colorful floras of very small ephemeral plants.

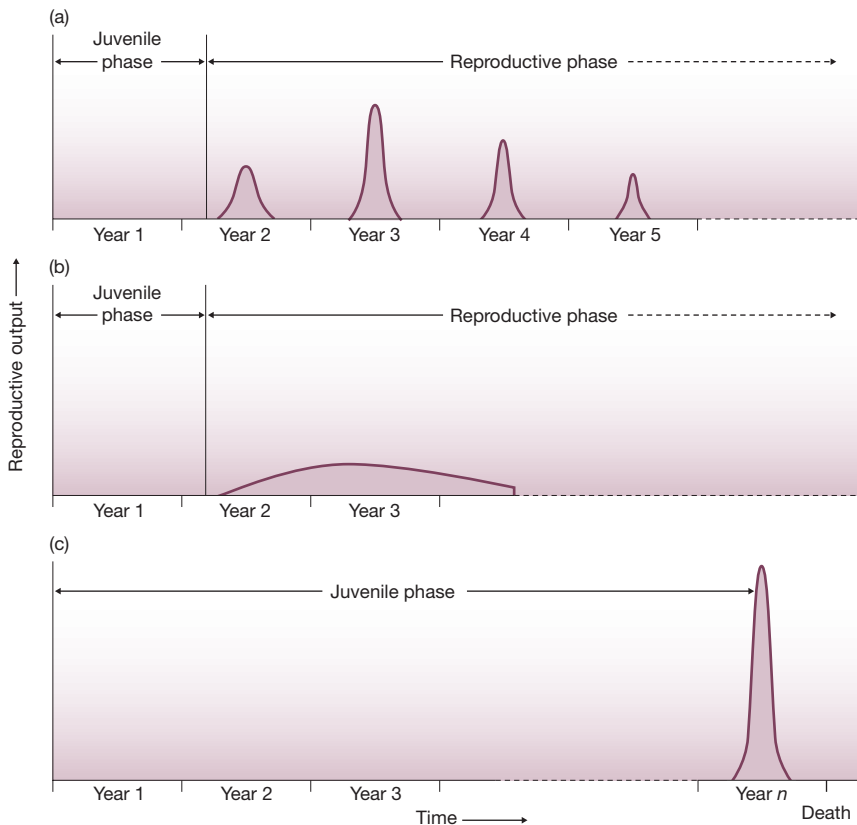
### 5.2.3 Longer life cycles

repeated, seasonal breeders

There is a marked seasonal rhythm in the lives of many long-lived plants and animals, especially in their reproductive activity: a period of reproduction once per year (Figure 5.7a). Mating (or the flowering of plants) is commonly triggered by the length of the *photoperiod* – the light phase in the daily light–dark cycle, which varies continuously through the year – and usually makes sure that young are born, eggs hatch or seeds are ripened when seasonal resources are likely to be abundant.

In populations of perennial species, the generations overlap and individuals of a range of ages breed side by side. The population is maintained in part by survival of adults and in part by new births. A study of the great tit *Parus major*, for example, showed that of 50 eggs that were laid by a breeding population of 10 birds in one season, only 30 hatchlings survived to become fully fledged, and



**Figure 5.7**

Simplified life histories for organisms living more than 1 year. (a) An iteroparous species breeding seasonally once per year. Death tends not to occur predictably after any given time, though a decline toward senescence is often observed. (b) An iteroparous species breeding continuously throughout the year. The pattern of death and decline is similar to that in (a). (c) A semelparous species passing several or many years in a pre-reproductive juvenile phase, followed by a burst of reproduction, followed in turn by inevitable death.

only three of these survived to adulthood the following year. These three 1-year-old birds were joined in that second year, though, by a further five birds aged between 2 and 5 years – the survivors of the previous year's 10 (Figure 5.8).

In wet equatorial regions, on the other hand, where there is very little seasonal variation in temperature and rainfall and scarcely any variation in photoperiod, we find species of plant that are in flower and fruit throughout the year – and continuously breeding species of animal that subsist on this resource (Figure 5.7b). There are several species of fig (*Ficus*), for instance, that bear fruit continuously and form a reliable year-round food supply for birds and primates. In more seasonal climates, humans are unusual in also breeding continuously throughout the year, though numbers of other species, cockroaches for example, do so in the stable environments that humans have created.

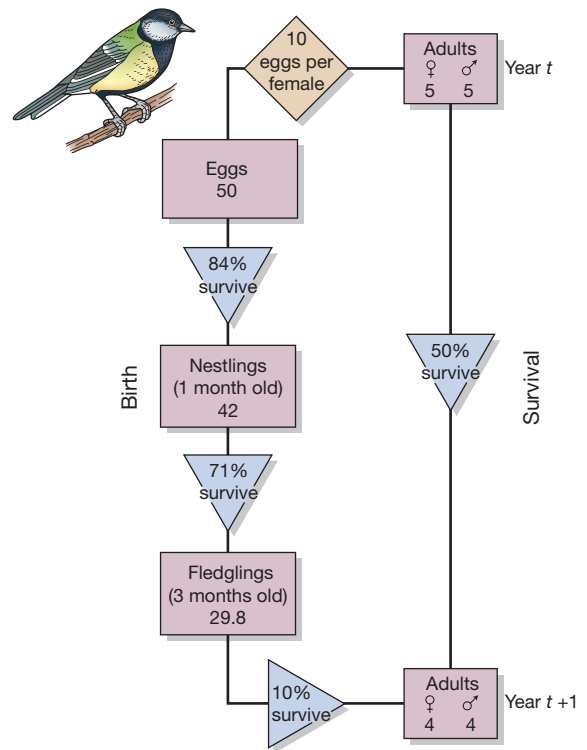
Other plants and animals (Figure 5.7c) may spend almost all their lives in a long non-reproductive (juvenile) phase and then have one lethal burst of reproductive activity. We saw such semelparity earlier in biennial plants, but it is also characteristic of some species that live much longer than 2 years. The Pacific salmon is a familiar example. Salmon are spawned in rivers. They spend the first phase of their juvenile life in fresh water and then migrate to the sea, often traveling thousands of miles. At maturity they return to the stream in which they were hatched. Some mature and return to reproduce after only 2 years at sea; others mature more slowly and return after 3, 4 or 5 years. At the time of

continuous breeders

semelparous species like salmon and bamboo

**Figure 5.8**

A diagrammatic life history for a population of great tits near Oxford, UK. Individuals typically live for several years; hence, the population in any one year is a combination of survivors from previous years and newborn individuals. Population sizes (in rectangles) are per hectare; the proportions surviving from one stage to the next are in triangles; the rate of egg production per female is shown in the diamond.



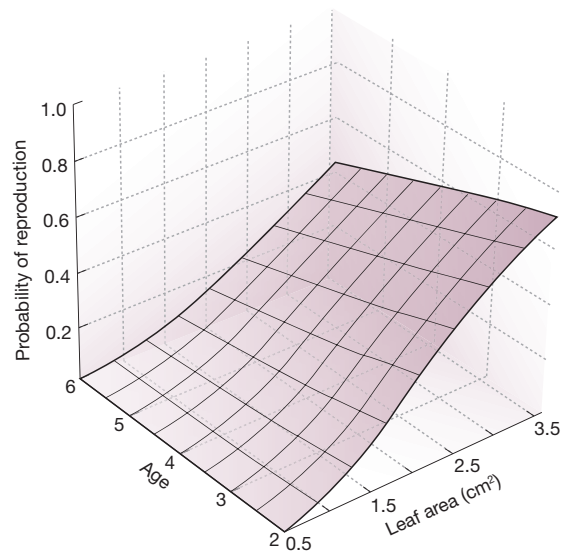
AFTER PERRINS, 1965

reproduction, the population of salmon is composed of overlapping generations of individuals. But all are semelparous: they lay their eggs and then die; their bout of reproduction is terminal.

There are even more dramatic examples of species that have a long life but reproduce just once. Many species of bamboo form dense clones of shoots that

**Figure 5.9**

The effect of plant age (years) and plant size (as measured by leaf area) on the probability of *Rhododendron lapponicum* shoots entering their reproductive phase. The relationships have been 'smoothed' by a statistical technique called 'logistic regression'. Note that the probability of reproduction increases with plant size at all ages. Also, older shoots are overall more likely to enter their reproductive phase because they tend to be bigger. However, at any given size, the probability of reproduction tends to *decrease* with age, making age itself a much poorer predictor of shoot fate than size.



AFTER KARLSSON &amp; JACOBSON, 2001

remain vegetative for many years: in some species, 100 years. The whole population of shoots then flowers simultaneously in a mass suicidal orgy. Even when shoots have become physically separated from each other, the parts still flower synchronously.

Organisms of long-lived species that are the same age, however, are not necessarily the same size – especially in modular organisms. Some individuals may be very old but have been suppressed in their growth and development by predators or by competition. Age, then, is often a particularly poor predictor of fecundity. An analysis that classifies the members of a population according to their size rather than their age (Figure 5.9) is often more useful in suggesting whether they will survive or reproduce.

size matters

### 5.3 Monitoring birth and death: life tables and fecundity schedules

The previous sections have outlined the different patterns of births and deaths in different species. But patterns are just a start. What are the *consequences* of these patterns in specific cases in terms of their effects on how a population might grow to pest proportions, say, or shrink to the brink of extinction? To determine these consequences, we need to monitor the patterns in a quantitative way.

There are different ways of doing so. To monitor and quantify survival, we may follow the fate of individuals from the same *cohort* within a population: that is, all individuals born within a particular period. A *cohort life table* then records the survivorship of the members of the cohort over time (Box 5.2). A different approach is necessary when we cannot follow cohorts but we know the ages of all the individuals in a population. We can then, at one time, describe the numbers of survivors of different ages in what is called a *static life table* (Box 5.2).



## 5.2 Quantitative aspects

### The basis for cohort and static life tables

In Figure 5.10, a population is portrayed as a series of diagonal lines, each line representing the life 'track' of an individual. As time passes, each individual ages (moves from bottom left to top right along its track) and eventually dies (the dot at the end of the track). Here, individuals are classified by their age. In other cases it may be more appropriate to split the life of each individual into different developmental stages.

Time is divided into successive periods:  $t_0$ ,  $t_1$ , etc. In the present case, three individuals were born (started

their life track) prior to the time period  $t_0$ , four during  $t_0$ , and three during  $t_1$ . To construct a *cohort life table*, we direct our attention to a particular cohort (in this case, those born during  $t_0$ ) and monitor what happens subsequently to the cohort. The life table is constructed by noting the number surviving to the start of each time period. Here, two of the four individuals survived to the beginning of  $t_1$ ; only one of these was alive at the beginning of  $t_2$ ; and none survived to the start of  $t_3$ . The first data column of the cohort life table

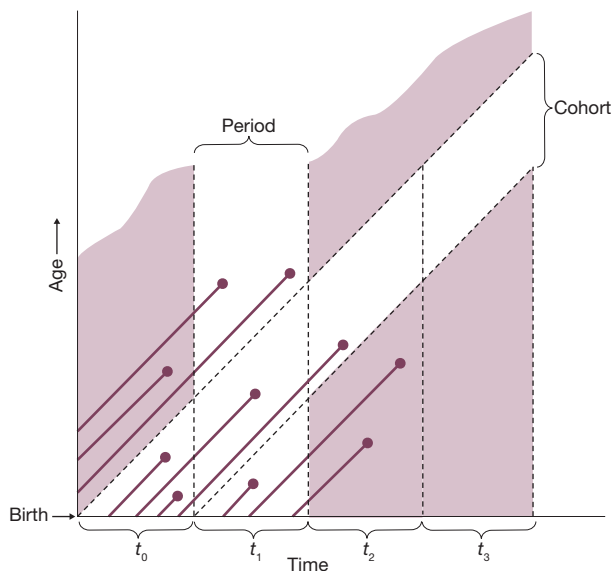


Figure 5.10

See text for details.

thus comprises the series of declining numbers in the cohort: 4, 2, 1, 0.

A different approach is necessary when we cannot follow cohorts but we know the ages of all the individuals in a population (perhaps from some clue such as the condition of the teeth in a species of deer). We can then, as the figure shows, direct our attention to the whole population during a single period (in this case,  $t_1$ ) and note the numbers of survivors of different ages in the population. These may be thought of as entries in a life table *if* we assume that rates of birth and death

are, and have previously been, constant – a very big assumption. What results is called a *static life table*. Here, of the seven individuals alive during  $t_1$ , three were actually born during  $t_1$  and are hence in the youngest age group, two were born in the previous time interval, two in the interval before that, and none in the interval before that. The first data column of the static life table thus comprises the series 3, 2, 2, 0. This amounts to saying that over these time intervals, a typical cohort will have started with three and declined over successive time intervals to two, then two again, then zero.

The fecundity of individuals also changes with their age, and to understand properly what is going on in a population we need to know how much individuals of different ages contribute to births in the population as a whole: these can be described in *age-specific fecundity schedules*.

### 5.3.1 Cohort life tables

an annual life table for a plant

The most straightforward life table to construct is a cohort life table for annuals, because with non-overlapping generations it is indeed often possible to follow a single cohort from the first birth to the death of the last survivor. One such life table, for the annual plant *Phlox drummondii*, is shown in Table 5.1. An initial cohort of 996 seeds was followed from seed germination to the death of the last adult, with the life cycle broken down into successive periods of 14–63 days.

Table 5.1

A simplified cohort life table for the annual plant *Phlox drummondii*. The columns are explained in the text.

AGE INTERVAL (DAYS) $x-x'$	NUMBER SURVIVING TO DAY $x$ $a_x$	PROPORTION OF ORIGINAL COHORT SURVIVING TO DAY $x$ $l_x$	SEEDS PRODUCED IN EACH STAGE $F_x$	SEEDS PRODUCED PER SURVIVING INDIVIDUAL IN EACH STAGE $m_x$	SEEDS PRODUCED PER ORIGINAL INDIVIDUAL IN EACH STAGE $l_x m_x$
0–63	996	1.000	0.0	0.00	0.00
63–124	668	0.671	0.0	0.00	0.00
124–184	295	0.296	0.0	0.00	0.00
184–215	190	0.191	0.0	0.00	0.00
215–264	176	0.177	0.0	0.00	0.00
264–278	172	0.173	0.0	0.00	0.00
278–292	167	0.168	0.0	0.00	0.00
292–306	159	0.160	53.0	0.33	0.05
306–320	154	0.155	485.0	3.13	0.49
320–334	147	0.148	802.7	5.42	0.80
334–348	105	0.105	972.7	9.26	0.97
348–362	22	0.022	94.8	4.31	0.10
362–	0	0.000	0.0	0.00	0.00
Total			2408.2		2.41

$$R_0 = \sum l_x m_x = \frac{\sum F_x}{a_0} = 2.41.$$

Even when generations overlap, if individuals can be marked early in their life so that they can be recognized subsequently, it can be possible to follow the fate of each year's cohort separately. It is then possible to merge the cohorts from the different years so as to derive a cohort life table that combines information from the whole study period. An example is shown in Table 5.2: females from a population of the yellow-bellied marmot, *Marmota flaviventris*, which was live-trapped and marked individually from 1962 through to 1993 in the East River Valley of Colorado.

The first column in each life table is a list of the age classes (or in some cases, stages) of the organism's life: 14–63-day periods for *Phlox*, years for the marmots. The second column is then the raw data from each study, collected in the field. It reports the number of individuals surviving to the beginning of each age class (see Box 5.2).

Ecologists are typically interested not just in examining populations in isolation but in comparing the dynamics of two or more perhaps rather different populations (in the presence and absence of a pollutant, for instance). Hence, it is necessary to standardize the raw data so that comparisons can be made. This is done in the third column of the table, which is said to contain  $l_x$  values, where  $l_x$  is defined as the proportion of the original cohort surviving to the start of age class. The first value in the third column,  $l_0$  (spoken: L zero), is therefore the proportion surviving to the beginning of this original age class. Obviously, in Tables 5.1 and 5.2, and in every life table,  $l_0$  is 1.00 (the whole cohort is there at the start).

In the marmots, for example, there were 773 females observed in this youngest age class. The  $l_x$  values for subsequent age classes are then expressed as proportions

a cohort life table for  
marmots . . .

Table 5.2

A simplified cohort life table for female yellow-bellied marmots, *Marmota flaviventris*, in Colorado. The columns are explained in the text.

AGE CLASS (YEARS) $x$	NUMBER ALIVE AT THE START OF EACH AGE CLASS $a_x$	PROPORTION OF ORIGINAL COHORT SURVIVING TO THE START OF EACH AGE CLASS $l_x$	NUMBER OF FEMALE YOUNG PRODUCED BY EACH AGE CLASS $F_x$	NUMBER OF FEMALE YOUNG PRODUCED PER SURVIVING INDIVIDUAL IN EACH AGE CLASS $m_x$	NUMBER OF FEMALE YOUNG PRODUCED PER ORIGINAL INDIVIDUAL IN EACH AGE CLASS $l_x m_x$
0	773	1.000	0	0.000	0.000
1	420	0.543	0	0.000	0.000
2	208	0.269	95	0.457	0.123
3	139	0.180	102	0.734	0.132
4	106	0.137	106	1.000	0.137
5	67	0.087	75	1.122	0.098
6	44	0.057	45	1.020	0.058
7	31	0.040	34	1.093	0.044
8	22	0.029	37	1.680	0.049
9	12	0.016	16	1.336	0.021
10	7	0.009	9	1.286	0.012
11	3	0.004	0	0.000	0.000
12	2	0.003	0	0.000	0.000
13	2	0.003	0	0.000	0.000
14	2	0.003	0	0.000	0.000
15	1	0.001	0	0.000	0.000
Total			519		0.670

$$R_0 = \sum l_x m_x = \frac{\sum F_x}{a_0} = 0.67.$$

of this number. Only 420 individuals survived to reach their second year (age class 1: between 1 and 2 years of age). Thus, in Table 5.2, the second value in the third column,  $l_1$ , is the proportion  $420/773 = 0.543$  (that is, only 0.543 or 54.3% of the original cohort survived this first step). In the next row,  $l_2 = 208/773 = 0.269$ , and so on. For *Phlox* (Table 5.1),  $l_1 = 668/996 = 0.671 = 67.1\%$  survived the first step.

In a full life table, subsequent columns would then use these same data to calculate the proportion of the original cohort that died at each stage and also the mortality rate for each stage, but for brevity these columns have been omitted here.

... and fecundity schedule ...

Tables 5.1 and 5.2 also include fecundity schedules for *Phlox* and for the marmots (columns 4 and 5). Column 4 in each case shows  $F_x$ , the total number of the youngest age class produced by each subsequent age class: this youngest class being seeds for *Phlox* and, for the marmots, independent juveniles fending for themselves outside of their burrows. Thus, *Phlox* plants produced seed between around day 300 and day 350 in the year; while marmots produced young when they were between 2 and 10 years old.

The fifth column is then said to contain  $m_x$  values, fecundity: the mean number of the youngest age class produced per surviving individual of each subsequent class. For *Phlox*, it is apparent that fecundity,  $m_x$ , the mean number of



seeds produced per surviving adult plant, reached a peak around day 340. For the marmots, fecundity was highest for 8-year-old females.

In the final column of a life table, the  $l_x$  and  $m_x$  columns are brought together to express the overall extent to which a population increases or decreases over time – reflecting the dependence of this on both the survival of individuals (the  $l_x$  column) and the reproduction of those survivors (the  $m_x$  column). That is, an age class contributes most to the next generation when a large proportion of individuals have survived and they are highly fecund, and it contributes least when few survive and/or they produce few (or no) offspring. The sum of all the  $l_x m_x$  values,  $\Sigma l_x m_x$ , where the symbol  $\Sigma$  means ‘the sum of’, is therefore a measure of the overall extent by which this population has increased or decreased in a generation. We call this the *basic reproductive rate* and denote it by  $R$ .

For *Phlox* (Table 5.1),  $R = 2.41$ : this population set approximately 2.5 times more seed at the end of the generation (the end of the season) than was present at the beginning. For the marmots,  $R = 0.67$ : the population was declining to around two-thirds its former size each generation. However, whereas for *Phlox* the length of a generation is obvious, since, being an annual, there is one generation each year, for the marmots the generation length must itself be calculated. The details of that calculation are beyond our scope here, but its value, 4.5 years, matches what we can observe ourselves in the life table: that a ‘typical’ period from an individual’s birth to giving birth itself (i.e. a generation) is around 4.5 years. Thus, Table 5.2 indicates that each generation, every 4.5 years, this particular marmot population was declining to around two-thirds its former size.

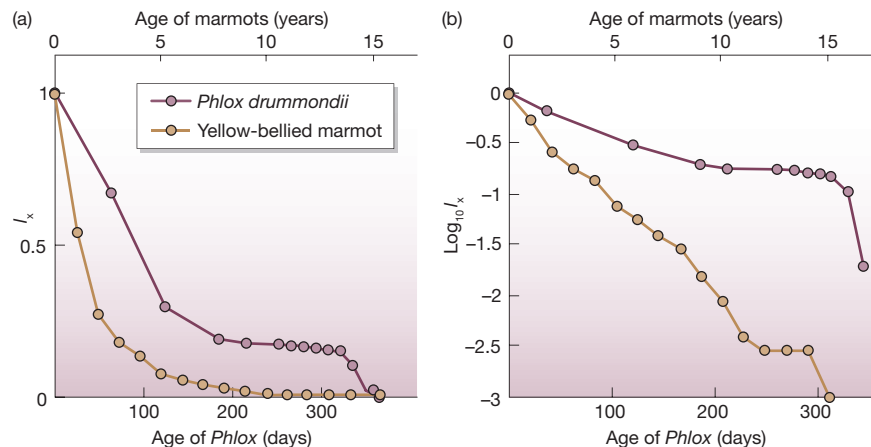
It is also possible to study the detailed pattern of decline in either the *Phlox* cohort or a cohort of marmots. Figure 5.11a, for example, shows the numbers surviving relative to the original population – the  $l_x$  values – plotted against the age of the cohort. However, this can be misleading. If the original population is 1000 individuals, and it decreases by half to 500 in one time interval, then this decrease looks more dramatic on a graph like Figure 5.11a than a decrease from 50 to 25 individuals later in the season. Yet the risk of death to individuals is the same on both occasions. If, however,  $l_x$  values are replaced by  $\log(l_x)$  values, that is, the logarithms of the values, as in Figure 5.11b (or, effectively the same thing, if  $l_x$  values are plotted on a log scale), then it is a characteristic of logs that the reduction of a population to half its original size will always look the same. *Survivorship curves* are, therefore, conventionally plots of  $\log(l_x)$  values against cohort age.

Figure 5.11b shows that there was a relatively rapid and constant decline in the size of the *Phlox* cohort over the first 6 months, but that the death rate thereafter remained steady and rather low until the very end of the season, when the survivors all died. For the marmots, Figure 5.11b shows an even more clearly constant decline until around the 10th year of life (when breeding ceased), followed by a brief period with effectively no mortality, after which the few remaining survivors died.

It is possible to see, therefore, even from these two examples, how life tables can be useful in characterizing the ‘health’ of a population – the extent to which it is growing or declining – and in identifying which stage in the life cycle (whether it is survival or birth) is apparently most instrumental in determining that rate of increase or decline. Either or both of these may be vital in determining how best to conserve an endangered species or control a pest.

... combined to give the basic reproductive rate

logarithmic survivorship curves



**Figure 5.11**

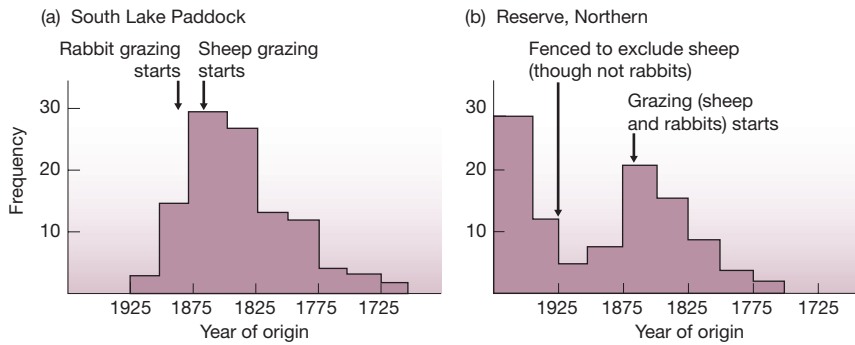
Following the survival of a cohort of *Phlox drummondii* (maroon, Table 5.1) and of the yellow-bellied marmot (yellow, Table 5.2). (a) When  $l_x$  is plotted against cohort age, it is clear that most individuals are lost relatively early in the lives of the cohorts, but there is no clear impression of the risk of mortality at different ages. (b) By contrast, a survivorship curve plotting  $\log(l_x)$  against age shows, for *Phlox*, that an initial 6 months of moderate survivorship was followed by an extended period of higher survivorship (less risk of mortality) and then by very low survivorship in the final weeks of the annual cycle. For the marmots, there was virtually constant mortality risk until around age 10, followed by a brief period of low risk after which the remaining survivors died.

### 5.3.2 Life tables for populations with overlapping generations

Many of the species for which we have important questions, and for which life tables may provide an answer, have repeated breeding seasons like the marmots, or continuous breeding as in the case of humans, but constructing life tables here is complicated, largely because these populations have individuals of many different ages living together. Building a cohort life table is sometimes possible, as we have seen, but this is relatively uncommon. Apart from the mixing of cohorts in the population, it can be difficult simply because of the longevity of many species.

a static life table – useful if used with caution

Another approach is to construct a ‘population snapshot’ in a static life table (see Box 5.2). Superficially, the data look like a cohort life table: a series of different numbers of individuals in different age classes. But great care is required: they can only be treated and interpreted in the same way if patterns of birth and survival in the population have remained much the same since the birth of the oldest individuals – and this will happen only rarely. Nonetheless, useful insights can sometimes be gained by combining the data from a static life table (an *age structure*: the numbers in different age classes) with corresponding background information. This is illustrated by a study of two populations of the long-lived tree *Acacia burkittii* in South Australia (Figure 5.12). Although differences in age structure between the populations are obvious, the reasons are not. Fortunately, background information provides important clues.



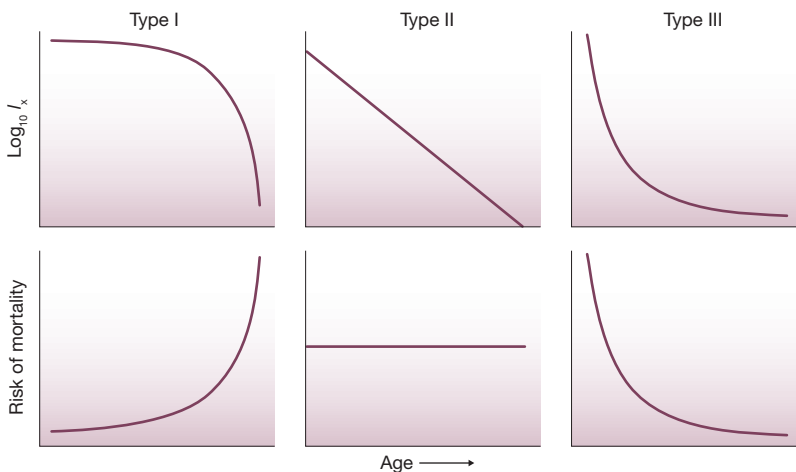
**Figure 5.12**

Age structures (and hence static life tables) of *Acacia burkittii* populations at two sites in South Australia. South Lake Paddock populations had been grazed by sheep from 1865 to 1970 and by rabbits from 1885 to 1970, whereas the Reserve population had been fenced in 1925 to exclude sheep (but did not exclude rabbits). With this information in hand, the effect of grazing from 1865 onward is evident in the decreased numbers of new recruits to both populations. However, the effects of fencing after 1925 are equally obvious in the Reserve population, where the proportion of new recruits increased dramatically. The effects of rabbit grazing on recruitment after fencing in the Reserve population can, however, still be detected, since, for example, the 1925–1940 age class was much smaller than the (pre-grazing) 1845–1860 class, even though the latter had survived an additional 75 years.

### 5.3.3 A classification of survivorship curves

Life tables provide a great deal of data on specific organisms. But ecologists search for generalities: patterns of life and death that we can see repeated in the lives of many species. Ecologists conventionally divide survivorship curves into three types, in a scheme that goes back to 1928, generalizing what we know about the way in which the risks of death are distributed through the lives of different organisms (Figure 5.13).

- In a type I survivorship curve, mortality is concentrated toward the end of the maximum lifespan. It is perhaps most typical of humans in developed countries and their carefully tended zoo animals and pets.

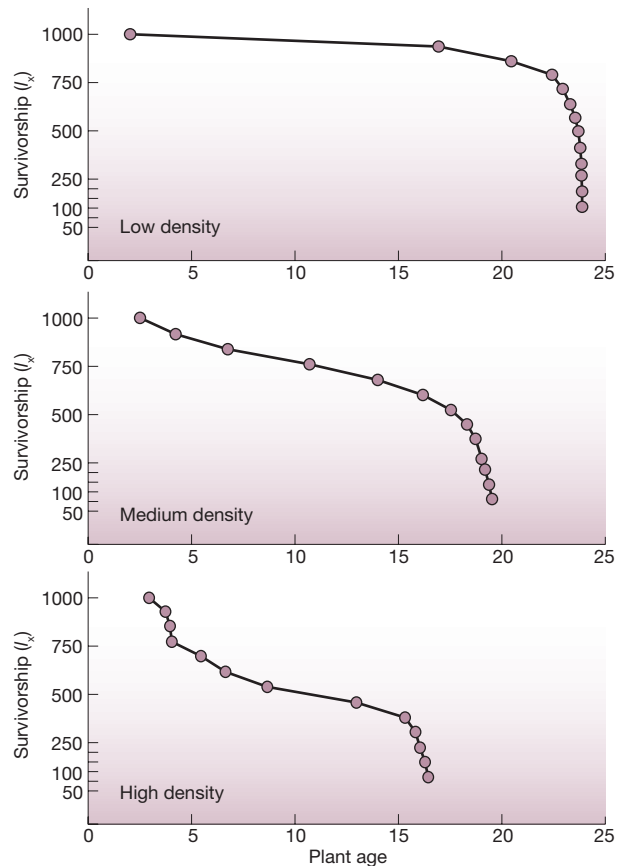


**Figure 5.13**

A classification of survivorship curves plotting  $\log(l_x)$  against age, above, with corresponding plots of the changing risk of mortality with age, below. The three types are discussed in the text.

**Figure 5. 14**

Survivorship curves for the sand dune annual plant *Erophila verna* monitored at three densities: high (initially 55 or more seedlings per 0.01 m<sup>2</sup> plot), medium (15–30 seedlings per plot) and low (1–2 seedlings per plot). The horizontal scale (plant age) is standardized to take account of the fact that each curve is the average of several cohorts, which lasted different lengths of time (around 70 days on average).



AFTER SYMONIDES, 1983

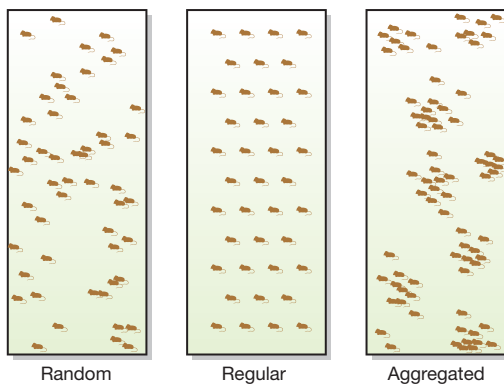
- A type II survivorship curve is a straight line signifying a constant mortality rate from birth to maximum age. It describes, for instance, the survival of buried seeds in a seed bank.
- In a type III survivorship curve there is extensive early mortality, but a high rate of subsequent survival. This is typical of species that produce many offspring. Few survive initially, but once individuals reach a critical size, their risk of death remains low and more or less constant. This appears to be the most common survivorship curve among animals and plants in nature.

These types of survivorship curve are useful generalizations, but in practice, patterns of survival are usually more complex. Thus, in a population of *Erophila verna*, a very short-lived annual plant inhabiting sand dunes, survival can follow a type I curve when the plants grow at low densities; a type II curve, at least until the last stages of life, at medium densities; and a type III curve in the early stages of life at the highest densities (Figure 5.14).

## 5.4 Dispersal and migration

patterns of distribution

Birth is only the beginning. If we were to stop there in our studies, many crucial ecological questions would remain unanswered. From their place of birth, all

**Figure 5.15**

Three generalized spatial patterns that may be exhibited by organisms across their habitat.

organisms move to locations where we eventually find them. Plants grow where their seeds fall, but seeds may be moved by the wind, water, animals or shifting soil. Animals move in search of food and safe havens, whether it is only to move 1 cm along a leaf from where their egg was deposited, or to move half-way around the globe. The effects of those movements are varied. In some cases they aggregate members of a population into clumps; in others they continually redistribute and shuffle them; and in still others they spread the individuals out. Three generalized spatial patterns that result from this movement – aggregated (clumped), random and regular (evenly) spaced – are illustrated in Figure 5.15. Clearly, movement and spatial distribution (the latter sometimes, confusingly, called ‘dispersion’) are intimately related.

Technically, the term *dispersal* describes the way individuals spread away from each other, such as when seeds are carried away from a parent plant or young lions leave the pride in search of their own territory. *Migration* refers to the mass directional movement of large numbers of a species from one location to another. Migration therefore describes the movement of locust swarms but also includes the smaller scale movements of intertidal organisms, back and forth twice a day, as they follow their preferred level of immersion or exposure.

Our view of dispersal and migration, and of the resulting distributions, is determined by the scale on which we are working. For example, consider the distribution of an aphid living on a particular species of tree in a woodland. On a large scale, the aphids appear to be aggregated in the woodlands and non-existent in the open fields. If the samples we took were smaller, and taken only in woodlands, the aphids would still appear to be aggregated, but now aggregated on their host trees rather than on trees in general. However, if samples were collected at an even smaller scale – the size of a leaf within a canopy – the aphids might appear to be randomly distributed over the tree as a whole. And on the scale experienced by the aphid itself (1 cm<sup>2</sup>), the distribution might appear regular as individuals on a leaf spread out to avoid one another (Figure 5.16).

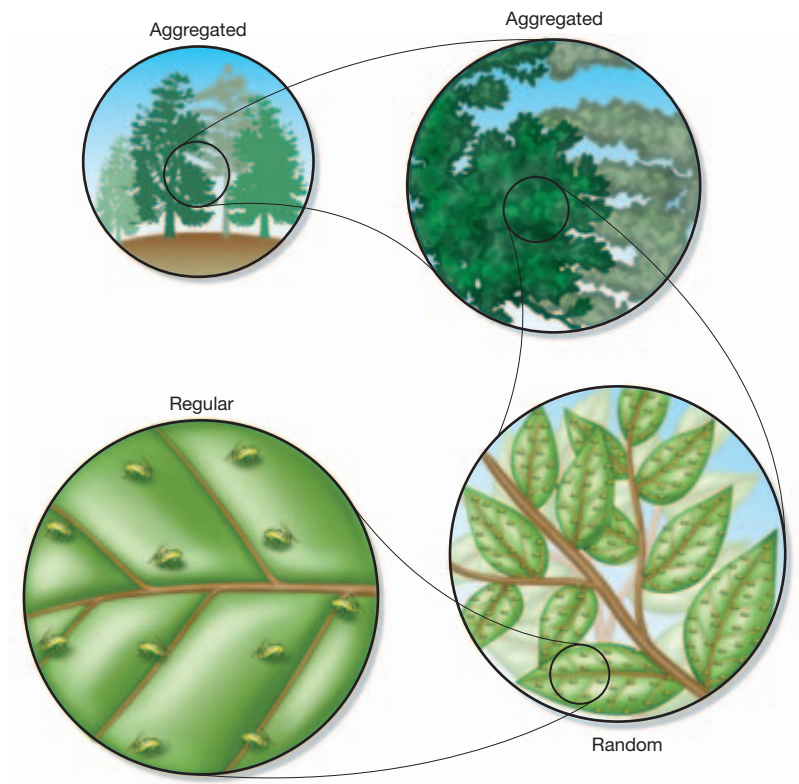
This example also illustrates the difference between the ‘average density’ and the crowding experienced by individuals in a population. The *average density* is simply the total number of individuals divided by the total size of the habitat – but it depends very much on how we define the habitat. For the aphids, if it includes everything, woodland and non-woodland, then average density will be low. It will be higher, but still quite low, if we include only woodland but every species of tree. It will be much higher, however, if we include only the aphids’ host trees.

the perception of pattern depends on the spatial scale

density and crowding

**Figure 5.16**

Are aphids distributed evenly, randomly or in an aggregated fashion? It all depends on the spatial scale at which they are viewed.



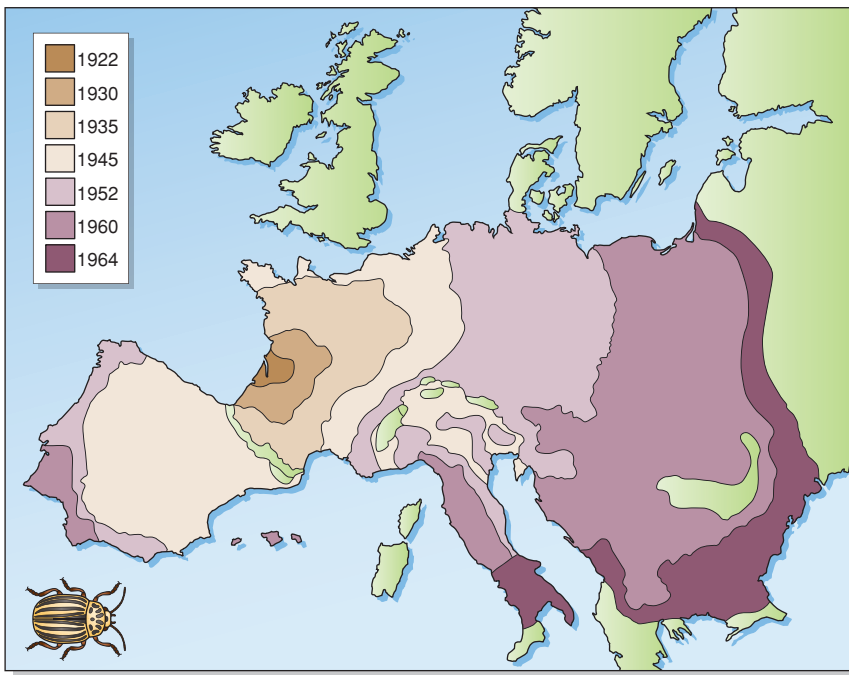
The average density of individuals in the United States is about 75 persons  $\text{km}^{-2}$ . Yet there are vast areas of the United States – rural and wilderness areas – within which the density is low, but also crowded cities and towns within which the density is much higher. And because the majority of people live in urban and suburban settings, the density actually experienced by people, on average, has been calculated at 3630 persons  $\text{km}^{-2}$ . There may be little impetus for dispersal, or migration, at the relatively low population pressure of 75 persons  $\text{km}^{-2}$ . At 3630 persons  $\text{km}^{-2}$ , however, individuals are much more likely to find ways to escape from their neighbors. Real measures of crowding as experienced by individuals are likely to be more important forces driving dispersal and migration than some average value of population density.

### 5.4.1 Dispersal determining abundance

dispersal: important but frequently neglected

Compared to birth and death, relatively few studies have examined the role of dispersal in determining the abundance of populations. However, studies that *have* looked carefully at dispersal have tended to bear out its importance. In a long-term and intensive investigation of a population of great tits, *Parus major*, near Oxford, UK, it was observed that 57% of breeding birds were immigrants rather than born in the population (Greenwood et al., 1978). And in a population of the Colorado potato beetle, *Leptinotarsa decemlineata*, in Canada, the average emigration rate of newly emerged adults was 97% (Harcourt, 1971). This makes the rapid spread of the beetle in Europe in the middle of the last century



**Figure 5.17**

Spread of the Colorado beetle (*Leptinotarsa decemlineata*) in Europe, 1922–1964.

AFTER JOHNSON, 1967

easy to understand (Figure 5.17). Indeed, most populations are more affected by immigration and emigration than is commonly imagined. Within the United States, for example, over 40% of US residents, over 100 million people, can trace their roots to the 12 million immigrants who entered the United States through the Ellis Island port from 1870 to 1920.

In fact, often the most important role played by dispersal in a population is to get the organisms there in the first place. For instance, the invasion of 116 patches of lowland heath vegetation in southern England by scrub and tree species was studied for the period from 1978 to 1987 (Figure 5.18). The most important factors accounting for such invasions were those describing the abundance of scrub and tree species in the vegetation bordering the heath patches. Invasions, and thus the subsequent dynamics of patches, were being driven by initiating acts of dispersal.

One key force provoking dispersal is the more intense competition suffered by crowded individuals (see Section 3.5) and the direct interference between such individuals even in the absence of a shortage of resources. We frequently observe, therefore, that the highest rates of dispersal are away from the most crowded patches (Figure 5.19): emigration dispersal is commonly density-dependent.

On the other hand, such density-dependent dispersal is by no means a general rule, and in some cases the converse pattern is observed – most dispersal at the lowest densities or *inverse* density dependence – a pattern often attributed to the avoidance of inbreeding between closely related individuals (and the lowered offspring fitness that would result), since on average, at low densities, a high proportion of those you grow up with are likely to be your close relatives. Furthermore, immigrants and emigrants not only influence the numbers in a population, they can also affect its composition. Dispersers are often the young, and males

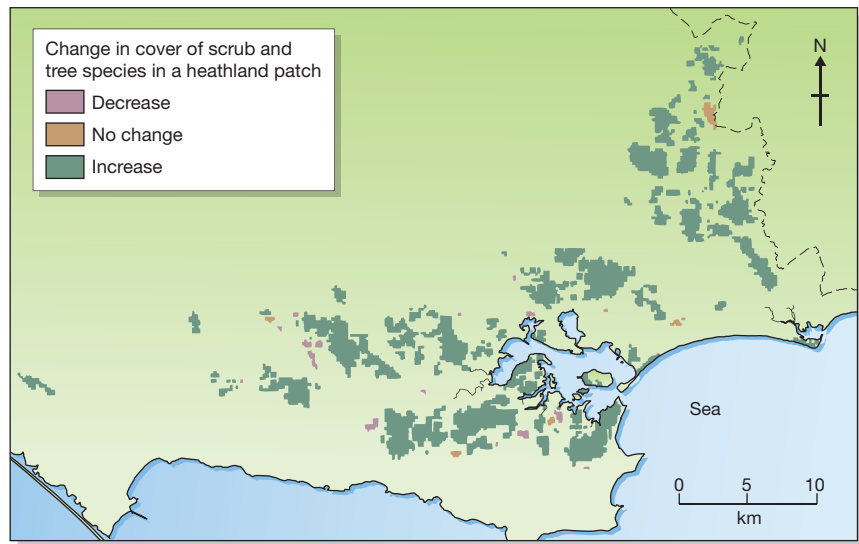
dispersal as invasion

density-dependent dispersal –  
and its converse

age- and sex-biased dispersal

**Figure 5.18**

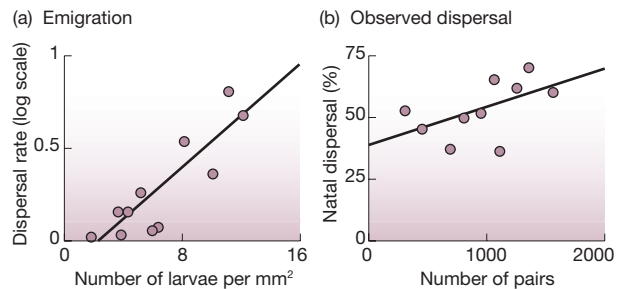
The invasion (i.e. increase in abundance) of most of the 116 patches of lowland heath in Dorset, UK by scrub and tree species between 1978 and 1987. The coastline is to the south and the county boundary to the east.



AFTER BULLOCK ET AL., 2002

**Figure 5.19**

Density-dependent dispersal. (a) The dispersal rates of newly hatched blackfly, *Simulium vittatum*, larvae increased with increasing density. (Data from Fonseca & Hart, 1996.) (b) The percentage of juvenile male barnacle geese, *Branta leucopsis*, dispersing from breeding colonies on islands in the Baltic Sea to non-natal breeding locations increased as density increased. (Data from van der Jeugd, 1999.)



AFTER SUTHERLAND ET AL., 2002

frequently do more moving about than females. In mammal dispersal, for instance, age and sex biases, and the forces of inbreeding avoidance and competition avoidance, may all be tied intimately together. Thus, in an experiment with gray-tailed voles, *Microtus canicaudus*, 87% of juvenile males and 34% of juvenile females dispersed within 4 weeks of initial capture at low densities, but only 16% and 12%, respectively, dispersed at low densities (Wolff et al., 1997). There was massive juvenile dispersal; this was particularly pronounced in males; and the especially high rates at low densities argue in favor of inbreeding avoidance as a major force shaping the pattern.

### 5.4.2 The role of migration

The mass movements of populations that we call migration are (rather like density-dependent dispersal) almost always from regions where the food resource is declining to regions where it is abundant (or where it will be abundant for the progeny). By day, planktonic plants live in the upper layers of the water in lakes where the light needed for photosynthesis is brightest. At night they migrate to lower, nutrient-rich depths. Crabs migrate along the shore with the tides, following the movement of their food supply as it is washed up in the waves. At longer time scales, some shepherds still follow the ages-old practice of ‘transhumance’,

moving their flocks of sheep and goats up to mountain pastures in summer and down again in the fall to track the seasonal changes in climate and food supply.

The long-distance migrations of terrestrial birds in many cases involve movement between areas that supply abundant food, but only for a limited time. They are areas in which seasons of comparative glut and famine alternate, and cannot support large all-year-round resident populations. For example, swallows (*Hirundo rustica*) migrate seasonally from northern Europe in the fall, when flying insects start to become rare, to South Africa when they are becoming common. In both areas the food supply that is reliable throughout the year can support only a small population of resident species. The seasonal glut supports the populations of invading migrants, which make a large contribution to the diversity of the local fauna.

## 5.5 The impact of intraspecific competition on populations

The concept of intraspecific competition was introduced in Section 3.5 because its intensity is typically dependent on resource availability. It re-emerges here because its effects are expressed through the focal topics of this chapter – rates of birth, death and movement. Competing individuals that fail to find the resources they need may grow more slowly or even die; survivors may reproduce later and less; or, as we have seen, if they are mobile, they may move farther apart or migrate elsewhere. Examples in which the dynamics of a species can be understood without a firm grasp of the effects of competition are rare.

The intensity of competition for limiting resources is often related to the density of a population, though, as we have seen, the straightforward density need not be a good measure of the extent to which its individuals are crowded. Modular sessile organisms are particularly sensitive to competition from their immediate neighbors: they cannot withdraw from each other and space themselves more evenly or escape by dispersal or migration. Thus, when silver birch trees (*Betula pendula*) were grown in small groups, there were more suppressed and dying branches on the sides of individual trees where their branches shaded each other than on the sides away from neighbors, where there was more vigorous growth (Figure 5.20).

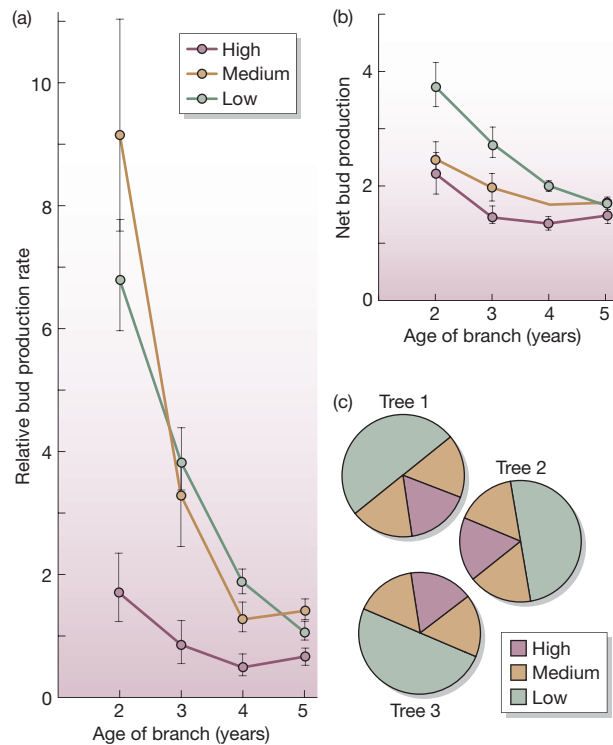
We saw in Section 3.5 that, over a sufficiently large density range, as density increases, competition between individuals generally reduces the per capita birth rate and increases the death rate, and that this effect is described as *density-dependent*. Thus, when birth and death rate curves are plotted against density on the same graph, and either or both are density-dependent, the curves must cross (Figure 5.21a–c). They do so at the density at which birth and death rates are equal, and because they are equal, there is no overall tendency at this density for the population either to increase or to decrease (ignoring, for convenience, both emigration and immigration). The density at the crossover point is called the *carrying capacity* and is denoted by the symbol  $K$ . At densities below  $K$ , births exceed deaths and the population increases. At densities above  $K$ , deaths exceed births and the population decreases. There is therefore an overall tendency for the density of a population under the influence of intraspecific competition to settle at  $K$ .

crowding not density – especially in modular organisms

density-dependent birth and death and the carrying capacity

**Figure 5.20**

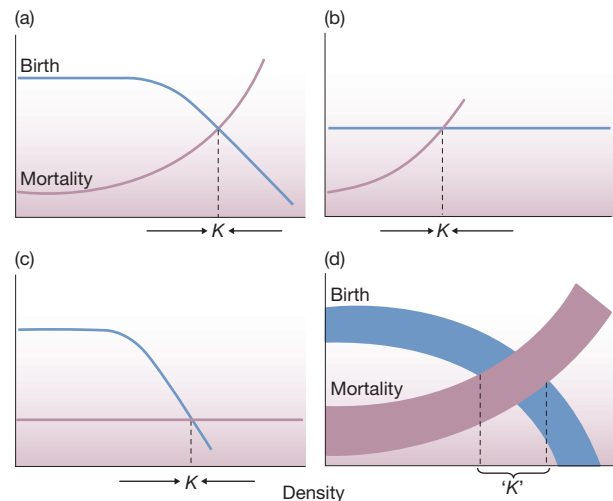
Mean relative bud production (new buds per existing bud) for silver birch trees (*Betula pendula*), expressed (a) as gross bud production and (b) as net bud production (birth minus death), in different interference zones (i.e. where they interfered to differing extents with their neighbors). (c) Plan of three trees, explaining these zones. ●, high interference; ○, medium; ○, low. Bars are standard errors.



AFTER JONES &amp; HARPER, 1987

**Figure 5.21**

Density-dependent birth and mortality rates lead to the regulation of population size. When both are density-dependent (a), or when either of them is (b, c), their two curves cross. The density at which they do so is called the *carrying capacity* ( $K$ ). However, the real situation is closer to that shown by the thick lines in (d), where mortality rate broadly increases, and birth rate broadly decreases, with density. It is possible, therefore, for the two rates to balance not at just one density, but over a broad range of densities, and it is toward this broad range ( $K'$ ) that other densities tend to move.



population regulation by competition – but not to a single carrying capacity

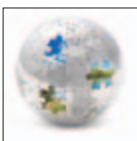
In fact, because of the natural variability within populations, the birth rate and death rate curves are best represented by broad lines, and  $K$  is best thought of not as a single density, but as a range of densities (Figure 5.21d). Thus, intraspecific competition does not hold natural populations to a single, predictable and unchanging level ( $K$ ), but it may act upon a very wide range of starting densities and bring them to a much narrower range of final densities. It therefore tends to

keep density within certain limits, and may thus be said to play a part in *regulating* the size of populations.

Of course, graphs like those in Figure 5.21 are generalizations on a grand scale. Many organisms, for example, have seasonal life cycles. For part of the year births vastly outnumber deaths, but later, after the period of peak births, there is likely to be a period of high juvenile mortality. Most plants, for example, die as seedlings soon after germination. Thus, although births may balance deaths over the year, a population that is ‘stable’ from year to year will often change dramatically over the seasons.

### 5.5.1 Patterns of population growth

When populations are sparse and uncrowded they may grow rapidly (and this can cause real problems – even with species that were previously endangered: Box 5.3). It is only as crowding increases that density-dependent changes in birth and death rates start to take effect. In essence, populations at these low



## 5.3 Topical ECOncerns

### Sea otter populations on the rise

It is estimated that as many as 300,000 sea otters once populated the North Pacific, from Russia to Mexico. But hunting caused the population to plummet to a few thousand by 1911. Since then, numbers have shot back up to more than 100,000, although the animals have not returned everywhere. The following newspaper article by Craig Welch concerns the situation along the Washington coastline in the northwest United States. It appeared in the *Philadelphia Inquirer* on March 4, 2001.



© ALAMY IMAGES ACRN42

#### Sea otters colliding with fishing industry

Sea otters are rebounding in dramatic fashion along Washington's coast, and that is forcing marine biologists and wildlife managers to prepare for a potentially uncomfortable collision between the charismatic critters and some coastal fisheries.

'It's a classic recipe for political polarization', said Glenn VanBlaricom, an associate professor of marine ecology at the University of Washington. 'People love sea otters, but they could run right into shellfish harvesters whose livelihoods depend on their food sources.' Wiped out of Washington waters in the 19th century by pelt-hungry hunters, otters have staged a comeback since being reintroduced to the western shores of the Peninsula in the late 1960s.

The population has grown 30-fold in as many years, and their range is expanding so far and fast that some scientists suspect groups of otters may someday – for the first time – make Puget Sound home.

... While sea otters remain protected under Washington state law as an endangered species, their numbers are increasing by 10 percent a year. The population now hovers at 600 animals, roughly a quarter of what marine experts think the environment can sustain.

But such a healthy return comes with complications. Because they lack blubber, otters eat a quarter of their weight each day to fuel their supercharged metabolisms. Their munchies of choice include the seafood humans crave – sea urchins, Dungeness crabs, clams, abalone. And their recent travels toward rich harvest areas such as the Dungeness Spit put them on a direct route toward multimillion-dollar commercial, recreational and tribal shellfisheries.

Steven Jeffries, who heads marine-mammal investigations for the State Department of Fish and Wildlife, said it was tough to determine whether it would be a few years or a few decades before conflicts begin.

(All content © 2001 Philadelphia Newspapers Inc. and may not be reprinted without permission.)

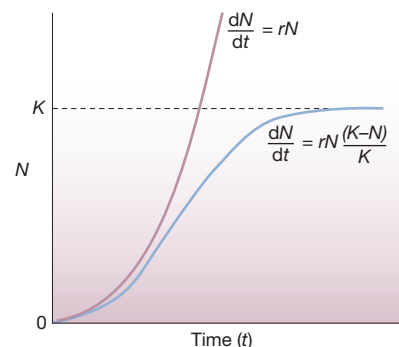
Consider the following options and debate their relative merits:

- 1 Shellfisheries are of considerable importance to commercial, recreational and tribal fishers. How would you weigh up the competing demands of conservation and fishing? Should the sea otters remain absolutely protected or is there a case for culling or some other form of control of their spread?
- 2 The story in Washington is very different from that in parts of Alaska, where otter numbers are declining, or Los Angeles, where recent efforts have been made to reintroduce the species. Suggest some plausible reasons for the different population trajectories in different areas.

densities grow by simple multiplication over successive intervals of time. This is *exponential* growth (Figure 5.22) and the rate of increase is the population's *intrinsic rate of natural increase* (denoted by  $r$ ; Box 5.4). Of course, any population that behaved in this way would soon run out of resources, but as we have seen, the rate of increase tends to become reduced by competition as the population grows, and it falls to zero when the population reaches its carrying capacity (since birth rate then equals death rate). A steady reduction in the rate of increase as densities move toward the carrying capacity gives rise to population growth that is not exponential but S-shaped (Figure 5.22). The pattern is also often called *logistic* growth after the so-called logistic equation (Box 5.4).

**Figure 5.22**

Exponential (maroon line) and S-shaped or *sigmoidal* (blue line) increases in the size of a population ( $N$ ) over time. These patterns describe the growth to be expected in general in populations in the absence (exponential) and under the influence (sigmoidal) of intraspecific competition, but are also generated, specifically, by the exponential and logistic equations shown (see also Box 5.4).







## 5.4 Quantitative aspects

### 5.4 QUANTITATIVE ASPECTS

#### The exponential and logistic equations of population growth

In this box, simple mathematical models are derived for populations first in the absence of, and then under the influence of, intraspecific competition. These and other mathematical models play an important part in ecology (see Chapter 1). They help us to follow through the consequences of assumptions we may wish to make, and to explore the behavior of ecological systems that we may find it hard to observe in nature or construct in the laboratory. The particular models in this box themselves form the basis for more complex models of *interspecific* competition and predation: they are important building blocks. It is essential to appreciate, however, that a pattern generated by such a model – for example, the S-shaped pattern of population growth under the influence of intraspecific competition – is not of interest, or important, because it is generated by the model. There are many other models that could generate very similar (indistinguishable) patterns. Rather, the point about the pattern is that it reflects important, underlying ecological processes – and the model is useful in that it appears to capture the essence of those processes.

We start with a model of a population in which there is no intraspecific competition and then incorporate that competition later. Our models are in the form of *differential equations*, describing the net rate of increase of a population, which will be denoted by  $dN/dt$  (spoken: DN by DT). This represents the speed at which a population increases in size,  $N$ , as time,  $t$ , progresses.

The increase in size of the whole population is the sum of the contributions of the various individuals within it. Thus, the average rate of increase per individual, or the per capita rate of increase (per capita means 'per head') is given by  $dN/dt \cdot (1/N)$ . In the absence of intraspecific competition (or any other force that increases the death rate or reduces the birth rate) this rate of increase is a constant and as high as it can be for the species concerned. It is called the *intrinsic rate of natural increase* and is denoted by  $r$ . Thus:

$$dN/dt(1/N) = r$$

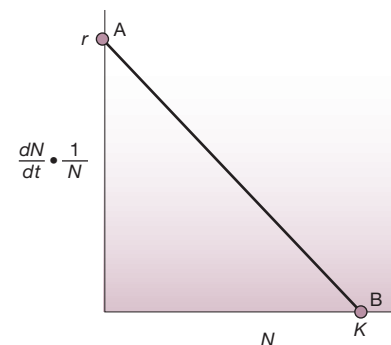
and the net rate of increase for the whole population is therefore given by:

$$dN/dt = rN$$

This equation describes a population growing *exponentially* (Figure 5.22).

Intraspecific competition can now be added. This we do by deriving the *logistic equation*, using the method set out in Figure 5.23. The net rate of increase per individual is unaffected by competition when  $N$  is very close to zero, because there is no crowding, nor a shortage of resources. It is still therefore given by  $r$  (point A). When  $N$  rises to  $K$  (the carrying capacity) the net rate of increase per individual is, by definition, zero (point B). For simplicity, we assume a straight line between A and B; that is, we assume a linear reduction in the per capita rate of increase, as a result of intensifying intraspecific competition, between  $N = 0$  and  $N = K$ .

Thus, on the basis that the equation for any straight line takes the form  $y = \text{intercept} + \text{slope } x$ , where  $x$  and



**Figure 5.23**

An ideal linear decline in the net rate of increase per individual with increasing population ( $N$ ).

y are the variates on the horizontal and vertical axes, here we have:

$$dN/dt(1/N) = r - (r/K)N$$

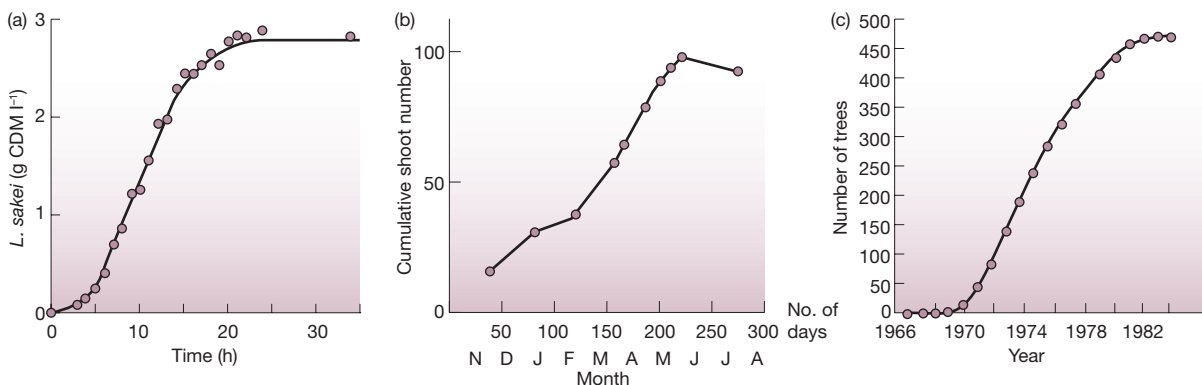
or, rearranging,

$$dN/dt = rN[1 - (N/K)]$$

This is the logistic equation, and a population increasing in size under its influence is shown in Figure 5.22. It describes a sigmoidal or S-shaped growth curve approaching a stable carrying capacity, but it is only one of many reasonable equations that do this. Its major advantage is its simplicity. Nevertheless, it has played a central role in the development of ecology.

The S-shaped curve can best be seen in action in laboratory studies of micro-organisms or animals with very short life cycles (Figure 5.24a). In these kinds of experiment it is easy to have experimental control of environmental conditions and resources. In the real world, outside the laboratory and the mind of the mathematician, the world is less simple. The complex life cycles of organisms, changing conditions and resources through the seasons, and the patchiness of habitats introduce many complications. In nature, populations often follow a very bumpy ride along the path of perfect logistic growth (Figure 5.24b), though not always (Figure 5.24c).

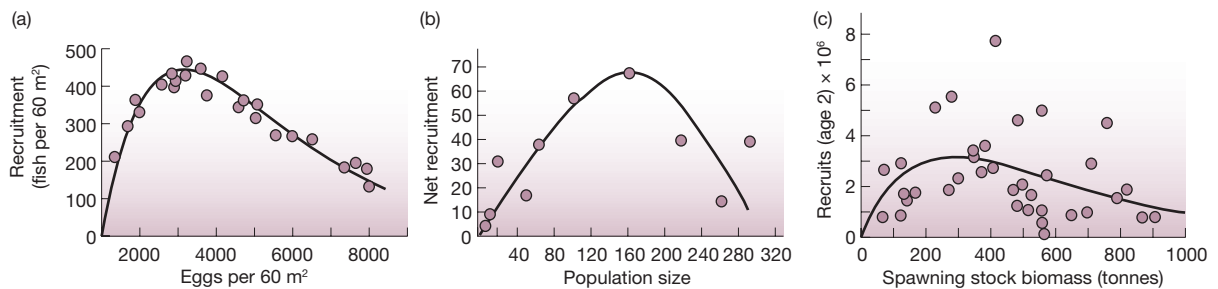
Another way to summarize the ways in which intraspecific competition affects populations is to look at *net recruitment* – the number of births minus the number of deaths in a population over a period of time. When densities are low, net recruitment will be low because there are few individuals available either to give birth or to die. Net recruitment will also be low at much higher densities as the carrying capacity is approached. Net recruitment will be at its peak, then, at some intermediate density. The result is a ‘humped’ or dome-shaped curve (Figure 5.25). Again, of course, as with the ideal logistic curve, real data from



**Figure 5.24**

Real examples of S-shaped population increase. (a) The bacterium *Lactobacillus sakei* [measured as grams of ‘cell dry mass’ (CDM) per liter] grown in nutrient broth. (b) The population of shoots (i.e. modules – see Section 5.1.1) of the annual plant *Juncus gerardi* in a salt marsh habitat on the west coast of France. (c) The population of the willow tree (*Salix cinerea*) in an area of land after myxomatosis had effectively prevented rabbit grazing.

(a) AFTER LEROY & DE VUYST, 2001; (b) AFTER BOUZILLE ET AL., 1997; (c) AFTER ALLIENDE & HARPER, 1989



**Figure 5.25**

Some dome-shaped net recruitment curves. (a) Six-month-old brown trout, *Salmo trutta*, in Black Brows Beck, England between 1967 and 1989. (b) An experimental population of the fruitfly *Drosophila melanogaster*. (c) 'Blackwater' herring, *Clupea harengus*, from the Thames estuary, England between 1962 and 1997.

(a) AFTER MYERS, 2001; FOLLOWING ELLIOTT, 1994; (b) AFTER PEARL, 1927; (c) AFTER FOX, 2001

nature never fall on a single line. But the dome-shaped curve reflects the essence of net recruitment patterns when density-dependent birth and death are the result of intraspecific competition.

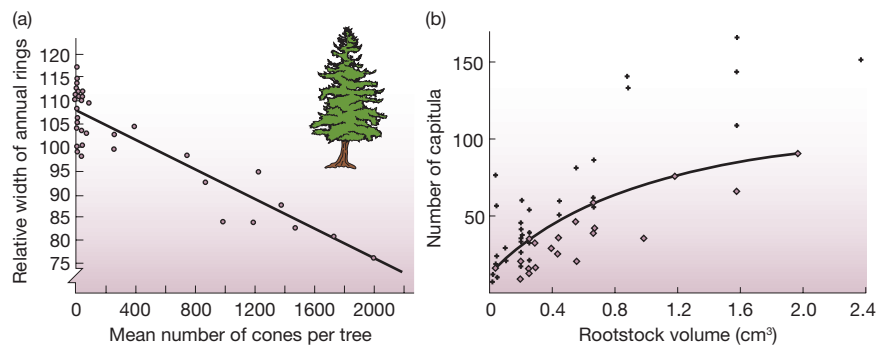
## 5.6 Life history patterns

One of the ways in which we can try to make sense of the world around us is to search for repeated patterns. In doing so, we are not pretending that the world is simple or that all categories are watertight, but we can hope to move beyond a description that is no more than a series of unique special cases. This final section of this chapter describes some simple, useful, though by no means perfect, patterns linking different types of life history and different types of habitat.

First, though, we return to a point made earlier: that in any life history there is a limited total amount of energy (or some other resource) available to an organism for growth and reproduction. Some trade-off may therefore be necessary: either grow more and reproduce less, or reproduce more and grow less. Specifically, there may be an observable cost of reproduction in that when reproduction starts, or increases, growth may slow or stop completely, as resources are diverted. We can, of course, look at this trade-off the other way around: an organism that makes vigorous growth, and so thrives in competition with its neighbors, may have to pay the price by reducing reproductive activity. In many forest trees, for example, growth rings in the trunk are conspicuously narrower in 'mast' years, when very heavy crops of seeds are produced (Figure 5.26a). Furthermore, as shown in Figure 5.26b, the diversion of resources to present reproduction may jeopardize subsequent survival (as also seen in the salmon and foxgloves described earlier), or simply reduce the capacity for future reproduction.

Yet it would be quite wrong to think that such negative, trade-off correlations abound in nature, only waiting to be observed. In particular, if there is variation between individuals in the amount of resource they have at their disposal, then there is likely to be a positive, not a negative, correlation between two apparently alternative processes – some individuals will be good at everything, others

the 'cost' of reproduction – a life history trade-off



**Figure 5.26**

(a) The negative correlation between cone crop size and annual growth increment for a population of Douglas fir *Pseudotsuga menziesii*. There is a cost of reproduction: the more the trees reproduce, the less they grow. (b) The cost of reproduction in ragwort plants (*Senecio jacobaea*). The line divides plants that survive (♦) from plants that have died by the end of the season (+). There are no surviving plants above and to the left of the line. For a given size (measured as 'rootstock volume') only those that have made the smallest reproductive allocation (measured as 'number of capitula') survive, although larger plants are able to make a larger allocation and still survive.

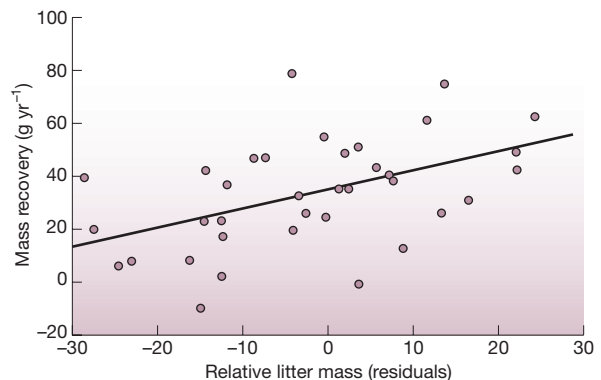
(A) AFTER EIS ET AL., 1965; (B) AFTER GILMAN & CRAWLEY, 1990

consistently awful. For instance, in Figure 5.27, the snakes in the best condition produced larger litters but also recovered from breeding more rapidly, ready to breed again.

But early reproduction can yield some striking rewards, particularly because the progeny themselves start reproduction earlier. Populations of individuals that reproduce early in their life can grow extremely fast – even if this means producing many fewer total offspring over their life than they would otherwise. The effect is shown by considering the life cycle of fruitflies (*Drosophila*). The number of eggs produced by a female in her lifetime is about 780. Doubling that number would clearly boost the intrinsic rate of increase, but such a massive increase in reproductive output is asking a great deal of an individual. So, what other changes in the life history of *Drosophila* would have a similar effect? In fact, the same rise in the rate of increase would be attained simply by shortening the juvenile period from around 10 to around 8.5 days (reproducing sooner,

**Figure 5.27**

Female asp viper (*Vipera aspis*) that produced larger litters ('relative' litter mass because total female mass was taken into account) also recovered more rapidly from reproduction (not 'relative' because mass recovery was not affected by size) ( $r = 0.43$ ;  $P = 0.01$ ).



rather than growing longer). Conversely, the rate of growth of populations can be slowed by delaying the onset of reproduction. One very effective way in which the growth rate of human populations can be slowed down, for example (see Chapter 12), is by discouraging early marriage and childbearing.

We can now turn to the life history patterns themselves. The potential of a species to multiply rapidly is advantageous in environments that are short-lived, allowing the organisms to colonize new habitats quickly and exploit new resources. This rapid multiplication is a characteristic of the life cycles of terrestrial organisms that invade disturbed land (for example, many annual weeds), or colonize newly opened habitats such as forest clearings, and of the aquatic inhabitants of temporary puddles and ponds. These are species whose populations are usually found expanding after the last disaster or exploiting the new opportunity. They have the life cycle properties that are favored by natural selection in such conditions: the production of large numbers of progeny, early in the life cycle, rather than investing heavily in either growth or survival. They have been called *r* species, because they spend most of their life in the near-exponential, *r*-dominated phase of population growth (see Box 5.4), and the habitats in which they are likely to be favored have been called *r*-selecting.

Organisms with quite different life histories survive in habitats where there is often intense competition for limited resources. The individuals that are successful in leaving descendants are those that have captured, and often held on to, the larger share of resources. Their populations are usually crowded and those that win in a struggle for existence do so because they have grown faster and/or larger (rather than reproducing) or have spent more of their resources in aggression or some other activity that has favored their survival under crowded conditions. They are called *K* species because their populations spend most of their lives in the *K*-dominated phase of population growth (see Box 5.4) – ‘bumping up’ against the limits of environmental resources – and the habitats in which they are likely to be favored have been called *K*-selecting.

A further common distinction between *r* and *K* species is whether they produce many small progeny (characteristic of *r* species) or few large progeny (characteristic of *K* species). This is another example of a life history trade-off: an organism has limited resources available for reproduction, and natural selection will influence how these are packaged. In environments where rapid population growth is possible, those individuals that produce large numbers of small progeny will be favored. The size of progeny can be sacrificed because they will usually not be in competition with others. However, in environments in which the individuals are crowded and there is competition for resources, those progeny that are well provided with resources by the parent will be favored. Producing progeny that are well endowed requires the trade-off of producing fewer of them (see, for example, Figure 5.28).

The *r/K* concept can certainly be useful in describing some of the general differences among different organisms. For instance, among plants it is possible to describe a number of very broad and general relationships (Figure 5.29). Trees in a forest are splendid examples of *K* species. They compete for light in the canopy, and survivors are those that put their resources into early growth and overtopping their neighbors. They usually delay reproduction until their branches have an assured place in the canopy of leaves. Once established they hold on to their position and usually have a very long life, with a relatively low allocation

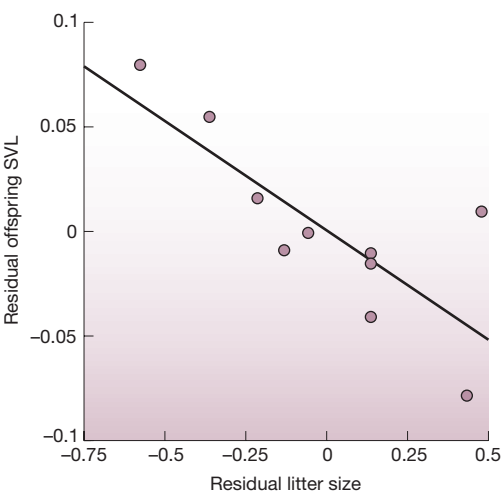
*r* and *K* species

*r*, *K* and progeny size and number

evidence for the *r/K* scheme?

Figure 5.28

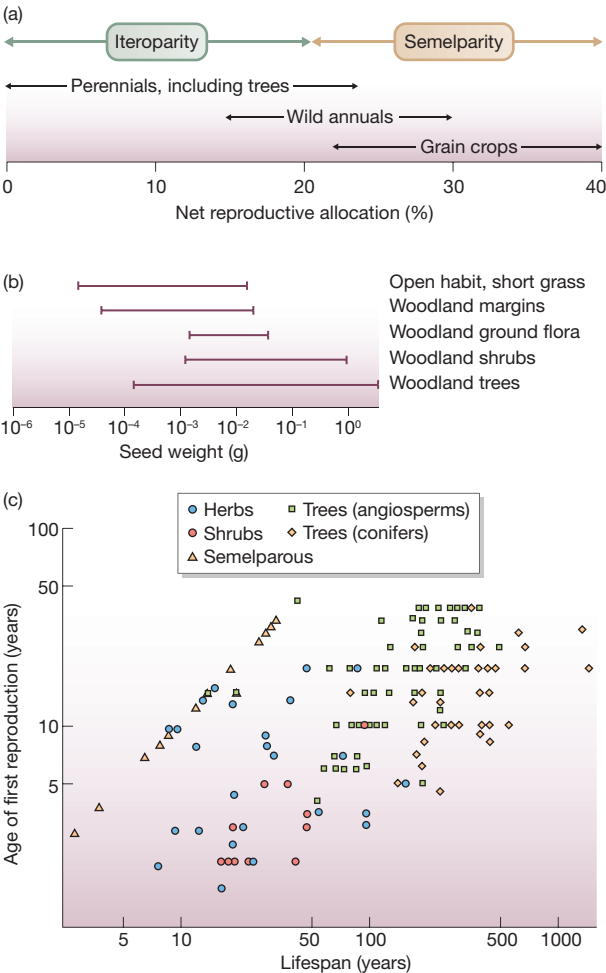
Evidence for a trade-off between the number of offspring produced in a clutch by a parent and the individual fitness of those offspring: a negative correlation between the size of offspring (as measured by their snout–vent length, SVL) and the number of them in a litter in the Australian highland copperhead snake, *Austrelaps ramsayi* ( $r^2 = 0.63$ ,  $P = 0.006$ ). ‘Residual’ offspring and litter sizes have been used: these are the values arrived at after variations in maternal size have been allowed for, since both increase with maternal size.



AFTER ROHR, 2001

Figure 5.29

Broadly speaking, plants show some conformity with the  $r/K$  scheme. For example, trees in relatively  $K$ -selecting woodland habitats: (a) have a relatively high probability of being iteroparous and a relatively small reproductive allocation; (b) have relatively large seeds; and (c) are relatively long-lived with relatively delayed reproduction.



AFTER HARPER, 1977; FROM SAUSBURY, 1942; OGDEN, 1968; HARPER & WHITE, 1974



to reproduction overall but large individual seeds. By contrast, in more disturbed, open,  $r$ -selecting habitats, the plants tend to conform to the general syndrome of  $r$  characteristics: a greater reproductive allocation, but smaller seeds, smaller size, earlier reproduction and a shorter life (Figure 5.29).

On the other hand, there seem to be about as many examples that fail to fit the  $r/K$  scheme as examples that correspond. One might regard this as a damning criticism of the  $r/K$  concept, since it undoubtedly demonstrates that the explanatory powers of the scheme are limited. But it is equally possible to regard it as very satisfactory that a relatively simple concept can help make sense of a large proportion of the multiplicity of life histories. Nobody, though, can regard the  $r/K$  scheme as the whole story. Like all attempts to classify species and their characteristics into pigeonholes, the distinction between  $r$  and  $K$  species has to be recognized as a convenient (and useful) human creation rather than an all-encompassing statement about the living world.



## Summary

### Counting individuals, births and deaths

Ecologists try to describe and understand the distribution and abundance of organisms. The processes that change the size of populations are birth, death and movement. A population is a number of individuals, but for some kinds of organism, especially modular organisms, it is not always clear what we mean by an individual.

Ecologists face enormous problems when they try to count what is happening to populations in nature. They almost always estimate rather than count. There are particular problems in counting modular organisms and the numbers of births and deaths.

### Life cycles and reproduction

The life histories of all unitary organisms can be seen as variations around a simple, sequential pattern. Some organisms fit several or many generations within a single year, some breed predictably just once each year (annuals), and others (perennials) have a life cycle extended over several or many years. Some, iteroparous species, breed repeatedly; others, semelparous species, have a single reproductive episode followed quickly by death.

Most annuals germinate or hatch in spring, grow rapidly, reproduce and then die before the end of summer. Most spend part of the year dormant. There is a marked seasonal rhythm in the lives of many long-lived species. Where there is very little seasonal variation, some reproduce throughout the year; others have a long non-reproductive phase and then one lethal burst of reproductive activity.

### Monitoring birth and death: life tables and fecundity schedules

Life tables can be useful in identifying what in a life cycle is apparently most instrumental in determining rates of increase or decline. A cohort life table records the survivorship of members of a single cohort. When we cannot follow cohorts, it may be possible to construct a static life table, but great care is required. The fecundity of individuals also changes with age, described in age-specific fecundity schedules.

Ecologists search for patterns of life and death that we can see repeated in the lives of many species. A useful set of survivorship curves (types I–III) has been developed, but in practice patterns of survival are usually more complex.

### Dispersal and migration

Dispersal is the way individuals spread away from each other. Migration is the mass directional movement of large numbers of a species from one location to another. Movement and spatial distribution are intimately related. Dispersal and migration can have a profound effect on the dynamics of a population and on its composition.

### The impact of intraspecific competition on populations

Over a sufficiently large density range, competition between individuals generally reduces the birth rate as density increases and increases the death rate (i.e. is density-dependent). Intraspecific competition therefore tends to keep density within certain limits and may thus be said to play a part in regulating the size of populations.

When populations are sparse and uncrowded they tend to exhibit exponential growth, but the rate of increase tends to become reduced by competition as the population grows, giving rise to population growth that is not exponential but S-shaped or logistic.

Intraspecific competition also affects net recruitment, typically resulting in a humped curve.

### Life history patterns

There is typically a limited total amount of energy or some other resource available to an organism for growth and reproduction. There may be an observable cost of reproduction. But populations of individuals that reproduce early in their life can grow extremely fast.

The potential of a species to multiply rapidly is favored by natural selection in environments that are short-lived, allowing the organisms to colonize new habitats quickly and exploit new resources. Such species have been called *r* species. Where there is often intense competition for limited resources, the individuals that are successful in leaving descendants are those that have captured the larger share of resources, often because they were born larger and/or have grown faster (rather than reproducing): so-called *K* species. The *r/K* concept can be useful in interpreting many of the differences in form and behavior of organisms, but of course it is not the whole story.

## Review questions

### REVIEW QUESTIONS

Asterisks indicate challenge questions

- 1 Contrast the meaning of the word 'individual' for unitary and modular organisms.
- 2 In a mark-recapture exercise during which a population of butterflies remained constant in size, an initial sample provided 70 individuals, each of which was marked and then released back into the population. Two days later, a second sample was taken, totaling 123 individuals of which 47 bore a mark from the first sample. Estimate the size of the population. State any assumptions that you have had to make in arriving at your estimate.
- 3\* Define annual, perennial, semelparous and iteroparous. Try to give an example of both an animal and a plant for each of the four possible combinations of these terms. In which cases is it difficult (or impossible) to come up with an example and why?
- 4 Contrast the derivation of cohort and static life tables and discuss the problems of constructing and/or interpreting each.
- 5 The following is an outline life table and fecundity schedule for a cohort of a population of sparrows. Fill in the missing values (wherever there is a question mark).

STAGE ( $x$ )	NUMBERS AT START OF STAGE ( $A_x$ )	PROPORTION OF ORIGINAL COHORT ALIVE AT START OF STAGE ( $l_x$ )	MEAN NO. OF EGGS PRODUCED PER INDIVIDUAL IN STAGE ( $m_x$ )
Eggs	173	?	0
Nestlings	107	?	0
Fledglings	64	?	0
1-year-olds	31	?	2.5
2-year-olds	23	?	3.7
3-year-olds	8	?	3.1
4-year-olds	2	?	3.5

$R = ?$

- 6 Describe what are meant by aggregated, random and regular distributions of organisms in space, and outline, with actual examples where possible, some of the behavioral processes that might lead to each type of distribution.
- 7\* Why is the average density of people in the United States lower than the density experienced by people, on average, in the United States? Is a similar contrast likely to apply to most species? Why? Under what conditions might it not apply?
- 8\* Compare unitary and modular organisms in terms of the effects of intraspecific competition both on individuals and on populations.
- 9 What is meant by the carrying capacity of a population? Describe where it appears, and why, in: (i) S-shaped population growth; (ii) the logistic equation; and (iii) dome-shaped net recruitment curves.
- 10 Explain why an understanding of life history trade-offs is central to an understanding of life history evolution. Explain the contrasting trade-offs expected to be exhibited by  $r$ -selected and  $K$ -selected species.

# Chapter 6



## Interspecific competition

### *Chapter contents*

#### CHAPTER CONTENTS

- 6.1 Introduction
- 6.2 Ecological effects of interspecific competition
- 6.3 Evolutionary effects of interspecific competition
- 6.4 Interspecific competition and community structure
- 6.5 How significant is interspecific competition in practice?

### *Key concepts*

#### KEY CONCEPTS

In this chapter you will:

- appreciate the difficulty of distinguishing between the power and importance of interspecific competition in principle and in practice
- distinguish between fundamental and realized niches
- define the Competitive Exclusion Principle and understand its limitations
- appreciate the potential role of the evolutionary effects of competition in species coexistence and the difficulty of proving that role
- understand the nature and importance of niche complementarity
- appreciate the difficulties of determining the prevalence of current competition in nature, and of distinguishing between the effects of competition and mere chance

*Interspecific competition is one of the most fundamental phenomena in ecology, affecting not only the current distribution and success of species but also their evolution. Yet the existence and effects of interspecific competition are often remarkably difficult to establish and demand an armory of observational, experimental and modeling techniques.*

## 6.1 Introduction

Having been introduced to *intraspecific* competition in previous chapters, it is not difficult to deduce what *interspecific* competition is. Its essence is that individuals of one species suffer a reduction in fecundity, survivorship or growth as a result of exploitation of resources or interference by individuals from another species. These competitive effects on individuals are likely to affect the population dynamics of the competing species. These, in turn, can influence the species' distributions and also their evolution. The distributions and abundances of species, of course, determine the compositions of the communities of which they are part. And evolution, in *its* turn, can influence the species' distributions and dynamics.

This chapter, then, is about both the ecological and the evolutionary effects of interspecific competition on individuals, on populations and on communities. But it also addresses a more general issue in ecology and indeed in science – that there is a difference between what a process can do and what it *does* do: a difference between what, in this case, interspecific competition is capable of doing and what it actually does in practice. These are two separate questions, and we must be careful to keep them separate.

two separate questions –  
the possible and actual  
consequences of competition

The way these different questions can be asked and answered will be different, too. To find out what interspecific competition is capable of doing is relatively easy. Species can be forced to compete in experiments, or they can be examined in nature in pairs or groups chosen precisely because they seem most likely to compete. But it is much more difficult to discover how important interspecific competition actually is. It will be necessary to ask how realistic our experiments were, how typical they were of the way species interact in nature, and how typical of pairs and groups of species generally were those singled out for special attention.

We begin, though, with some examples of what interspecific competition can do.

## 6.2 Ecological effects of interspecific competition

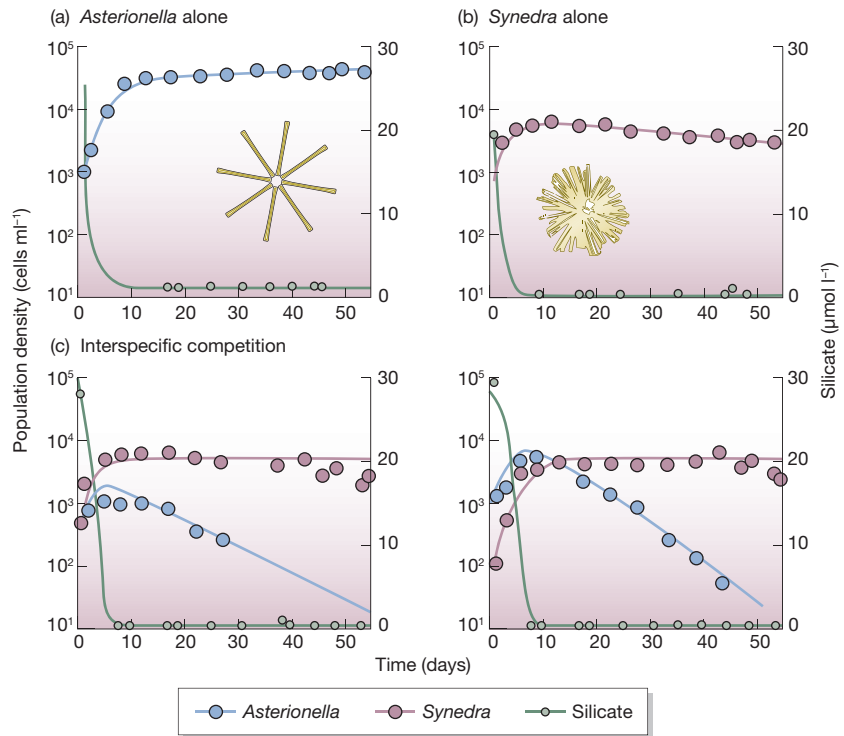
### 6.2.1 Competition between diatoms for silicate

Competition was investigated in the laboratory between two species of freshwater diatoms (single-celled plants), *Asterionella formosa* and *Synedra ulna*, both of which require silicate in the construction of their cell walls (see Section 3.5).

**Figure 6.1**

Competition between diatoms.

(a) *Asterionella formosa*, when grown alone in a culture flask, establishes a stable population and maintains a resource, silicate, at a constant low level.  
 (b) When *Synedra ulna* is grown alone it does the same, but maintains silicate at an even lower level.  
 (c) When grown together, in two replicates, *Synedra* drives *Asterionella* to extinction.



AFTER TILMAN ET AL., 1981

The population densities of the diatoms were monitored, but at the same time their impact on their limiting resource (silicate) was also being recorded. When either species was grown alone in a liquid medium to which resources were continuously being added, it established a steady population density while reducing the silicate to a constant low concentration (Figure 6.1a, b). However, in exploiting this resource, *Synedra* reduced the silicate concentration to a lower level than did *Asterionella*. Hence, when the two species were grown together, *Synedra* maintained the concentration at a level that was too low for the survival and reproduction of *Asterionella* and only *Synedra* survived (Figure 6.1c).

Thus, although both species were capable of living alone in the laboratory habitat, when they competed, *Synedra* excluded *Asterionella* because it was the more effective exploiter of their shared, limiting resource. A similar result has been obtained for the nocturnal, insectivorous gecko *Hemidactylus frenatus*, an invader of urban habitats across the Pacific basin, where it is responsible for population declines of the native gecko *Lepidodactylus lugubris* (Petren and Case, 1996). The diets of the two geckos overlap substantially and insects are a limiting resource for both. The invader is capable of depleting insect resources in experimental enclosures to lower levels than the native gecko, and the latter suffers reductions in body condition, fecundity and survivorship as a result.

### 6.2.2 Coexistence and exclusion of competing salmonid fishes

*Salvelinus malma* (Dolly Varden charr) and *S. leucomaenis* (white-spotted charr) are morphologically similar and closely related species of salmonid fish (see

more efficient exploiters exclude  
less efficient ones



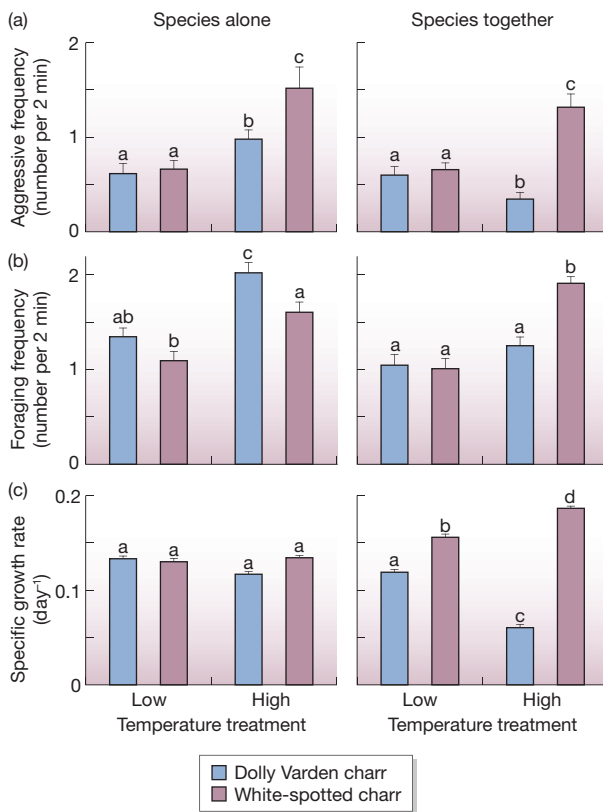


Figure 6.2

(a) Frequency of aggressive encounters initiated by individuals of each fish species during a 72-day experiment in artificial stream channels with two replicates each of 50 Dolly Varden (blue histograms) or 50 white-spotted charr (maroon histograms) alone (allopatry) or 25 of each species together (sympatry); (b) foraging frequency; and (c) specific growth rate in length. Different letters indicate means are significantly different from each other.

Section 3.2.4). They are found together in many streams on Hokkaido Island in Japan, but Dolly Varden are distributed further upstream than white-spotted charr, with a zone of overlap at intermediate altitudes. In streams where one species is absent, the other expands its range. Water temperature, which has profound consequences for fish ecology, increases downstream.

In laboratory streams, higher temperatures (12°C as compared to 6°C) led to increased aggression in both species when they were tested alone. But this effect was reversed for Dolly Varden when white-spotted charr were also present (Figure 6.2a). Reflecting this, Dolly Varden charr were suppressed from obtaining favorable foraging positions and so foraged far less effectively when white-spotted charr were present at the higher temperature (Figure 6.2b). Also, when alone, neither species' growth rates were influenced by temperature, but when both species were present, growth of Dolly Varden charr decreased with increasing temperature, whereas that of white-spotted charr increased (Figure 6.2c), such that the growth rate of Dolly Varden was much lower than that of white-spotted charr at the higher temperature.

These results are consistent with the hypothesis that the lower altitudinal boundary of Dolly Varden charr in the Japanese streams was due to temperature-mediated competition favoring white-spotted charr: they were more aggressive, foraged more effectively and grew far faster. But the results do not support the contention that the upper boundary of white-spotted charr is also due to temperature-mediated competitive difference; that is, Dolly Varden did not outcompete white-spotted charr in any of the experiments, even at the lower temperatures. Further

competitive advantage  
determined by temperature-  
dependent aggressive behaviour

work will be needed to determine why Dolly Varden exclude white-spotted charr upstream.

### 6.2.3 Some general observations

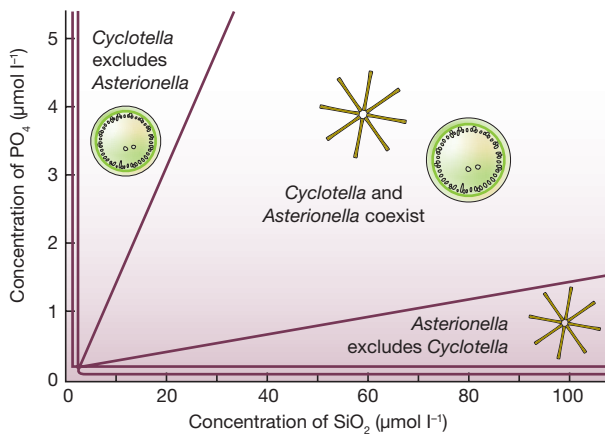
These two examples illustrate several points of general importance.

- 1 Competing species often coexist at one spatial scale but are found to have distinct distributions at a finer scale of resolution. Here, the fishes coexisted in the same stream, but each was more or less confined to its own altitudinal zone.
- 2 Species are often excluded by interspecific competition from locations at which they could exist perfectly well in the absence of interspecific competition. Here, Dolly Varden charr can live in the white-spotted charr zone – but only when there are no white-spotted charr there. Similarly, *Asterionella* can live in laboratory cultures – but only when there were no *Synedra* there.
- 3 We can describe this by saying that the conditions and resources provided by the white-spotted charr zone are part of the *fundamental niche* of Dolly Varden charr (see Section 3.6 for an explanation of ecological niches) in that the basic requirements for the existence of Dolly Varden charr are provided there. But the white-spotted charr zone does not provide a *realized niche* for Dolly Varden when white-spotted charr are present. Likewise, the laboratory cultures provided the requirements of the fundamental niches of both *Synedra* and *Asterionella*, but those of the realized niche for only *Synedra*.
- 4 Thus, a species' fundamental niche is the combination of conditions and resources that allow that species to exist, grow and reproduce when considered in isolation from any other species that might be harmful to its existence; whereas its realized niche is the combination of conditions and resources that allow it to exist, grow and reproduce in the presence of specified other species that might be harmful to its existence – especially interspecific competitors.
- 5 Competing species can therefore coexist when both are provided with a realized niche by their habitat (in the present case, the stream as a whole provided a realized niche for both fishes); but even in locations that provide a species with the requirements of its fundamental niche, that species may be excluded by another, superior competitor that denies it a realized niche there.
- 6 Finally, the fish study illustrates the importance of experimental manipulation if we wish to discover what is really going on in a natural population – 'nature' may need to be prodded to reveal its secrets.

fundamental and realized niches

### 6.2.4 Coexistence of competing diatoms

Another experimental study of competing diatoms looked at species coexisting on not one but two shared, limiting resources. The two species were *Asterionella formosa* (again) and *Cyclotella meneghiniana*, and the resources, which were both

**Figure 6.3**

*Asterionella formosa* and *Cyclotella meneghiniana* coexist when there are roughly balanced supplies of silicate ( $\text{SiO}_2$ ) and phosphate ( $\text{PO}_4$ ), but *Asterionella* excludes *Cyclotella* when there are especially low supplies of phosphate, whereas *Cyclotella* excludes *Asterionella* when there are especially low supplies of silicate.

capable of limiting the growth of both diatoms, were silicate and phosphate. However, whereas *Cyclotella* was the more effective exploiter of silicate (reducing its concentration to a lower level), *Asterionella* was the more effective exploiter of phosphate. Thus, in cultures where there were especially low supplies of silicate, *Cyclotella* excluded *Asterionella* (Figure 6.3): such cultures failed to provide a realized niche for *Asterionella*, the inferior competitor there. Conversely, in cultures where there were especially low supplies of phosphate, *Asterionella* excluded *Cyclotella*. However, in cultures with relatively balanced supplies of silicate and phosphate, the two diatoms coexisted (Figure 6.3): with two species, both provided with sufficient supplies of a resource on which they were superior, there was a realized niche for both.

### 6.2.5 Coexistence of competing birds

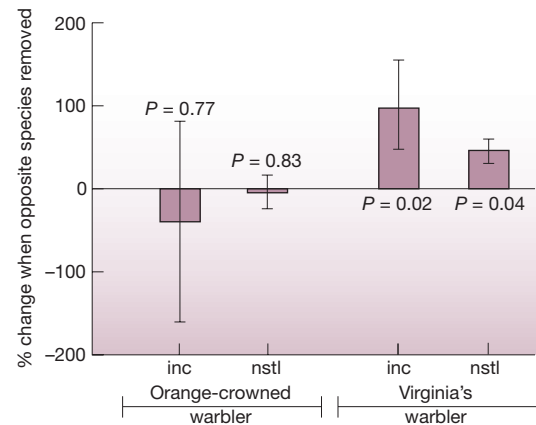
It is not always so easy to identify the ‘niche differentiation’ or ‘differential resource utilization’ that allows competitors to coexist. Ornithologists, for example, are well aware that closely related species of birds often coexist in the same habitat. For example, five *Parus* species occur together in English broad-leaved woodlands: the blue tit (*Parus caeruleus*), the great tit (*P. major*), the marsh tit (*P. palustris*), the willow tit (*P. montanus*) and the coal tit (*P. ater*). All have short beaks and hunt for food chiefly on leaves and twigs, but at times on the ground; all eat insects throughout the year, and also seeds in winter; and all nest in holes, normally in trees. Yet, the closer we look at the details of the ecology of such coexisting species, the more likely we are to find ecological differences – for example, in precisely where within the trees they feed, in the size of their insect prey and the hardness of the seeds they take. We may be tempted to conclude that such species compete but coexist by eating slightly different resources in slightly different ways: ‘differential resource utilization’. But in complex natural environments, such conclusions, while plausible, are difficult to prove.

Indeed, it is often not easy to prove even that the species compete. To do so, it is usually necessary to remove one or more of the species and monitor the responses of those that remain. This was done, for example, in a study of two very similar bird species: the orange-crowned warbler (*Vermivora celata*) and the virginia’s warbler (*V. virginiae*), whose breeding territories overlap in central

coexistence through niche differentiation – and even competition – may be difficult to prove

**Figure 6.4**

Percentage difference in feeding rates (mean  $\pm$  SE) at orange-crowned warbler and virginia's warbler nests on plots where the other species had been experimentally removed. Feeding rates (visits per hour to the nest with food) were measured during incubation (inc; rates of male feeding of incubating females on the nest) and during the nestling period (nstl; nestling feeding rates by both parents combined). *P*-values are from *t*-tests of the hypothesis that each species fed at higher rates on plots from which the other had been removed. This hypothesis was supported for virginia's warblers but not orange-crowned warblers.



AFTER MARTIN &amp; MARTIN, 2001

Arizona. On plots where one of the two species had been removed, the remaining species fledged between 78% and 129% more young per nest. The enhanced performance was due to improved access to preferred nest sites and consequent decreases in the loss of nestlings to predators. In the case of virginia's warblers, but not orange-crowned warblers, feeding rate also increased in plots from which the other species was removed (Figure 6.4).

### 6.2.6 Coexistence of competing rodents and ants

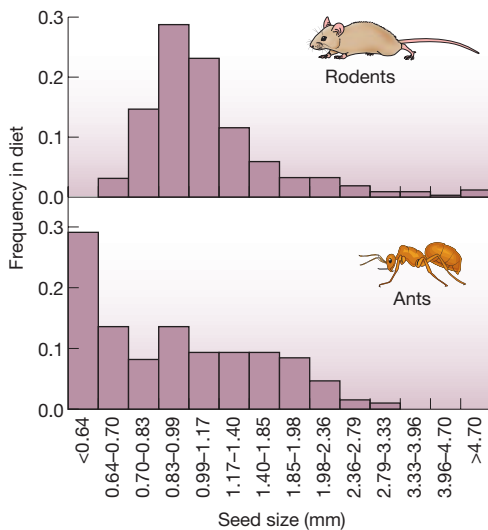
The examples described so far have all involved pairs of closely related species – diatoms, salmonid fish or birds. This is potentially misleading in at least two important respects. First, competition may occur amongst larger groups of species than just a pair – where it is sometimes, therefore, called ‘diffuse’ competition. And second, competition may occur between completely unrelated species.

competition between groups of unrelated species

Both points are illustrated by a study of interspecific competition involving seed-eating ants and seed-eating rodents in deserts of the southwestern United States. At the study sites, only two *guilds* (groups of species that feed on similar foods in a similar fashion; Root, 1967) fed on seeds: the rodents and the ants. By studying the size of the seeds harvested by each guild, it was apparent that the two exhibited significant overlap in the size of the seeds they ate (Figure 6.5). Ants did eat a larger proportion of the smallest seeds, but overall the potential for resource competition between them was very high.

As already noted, however, the only true test for whether competition occurs between them would be to manipulate the abundance of each competitor and observe the response of its counterpart. Consequently, eight plots were established in similar habitats. In two, rodents were trapped and excluded by fencing, to ensure that only ants now had access to the seeds. In another two, ants were eliminated by repeated applications of pesticides. In two further plots both ants and rodents were excluded, and finally two plots were maintained as unmanipulated controls.

When either rodents or ants were removed, there was a statistically significant increase in the numbers of the other guild: the depressive effect of interspecific competition from each guild on the abundance of the other was apparent. Also, when rodents were removed, the ants ate as many seeds as the rodents and ants

**Figure 6.5**

The diets of ants and rodents overlap: sizes of seeds harvested by coexisting ants and rodents near Portal, Arizona.

had previously eaten between them – as did the rodents when the ants were removed; only when both were removed did the amount of resource increase. In other words, under normal circumstances both guilds eat less and achieve lower levels of abundance than they would do if the other guild were absent. This clearly indicates that rodents and ants, although they coexist in the same habitat, compete interspecifically with one another.

### 6.2.7 The Competitive Exclusion Principle

The patterns that are apparent in these examples have also been uncovered in many others, and have been elevated to the status of a principle: the *Competitive Exclusion Principle* or Gause's Principle (named after an eminent Russian ecologist). It can be stated as follows:

- If two competing species coexist in a stable environment, then they do so as a result of niche differentiation, i.e. differentiation of their realized niches.
- If, however, there is no such differentiation, or if it is precluded by the habitat, then one competing species will eliminate or exclude the other.

Although the principle has emerged here from a contemplation of patterns evident in real sets of data, its establishment was – and many modern discussions of interspecific competition still are – bound up with a simple mathematical model of interspecific competition, usually known by the names of its two (independent) originators: Lotka and Volterra (Box 6.1).

There is no question that there is some truth in the principle that competitor species can coexist as a result of niche differentiation, and that one competitor species may exclude another by denying it a realized niche. But it is crucial also to be aware of what the Competitive Exclusion Principle does *not* say.

It does *not* say that whenever we see coexisting species with different niches it is reasonable to jump to the conclusion that this is the principle in operation. Each species, on close inspection, has its own unique niche. Niche differentiation

The Competitive Exclusion Principle – what it does and does not say



## 6.1 QUANTITATIVE ASPECTS

### 6.1 Quantitative aspects

#### The Lotka–Volterra model of interspecific competition

The most widely used model of interspecific competition is the Lotka–Volterra model (Volterra, 1926; Lotka, 1932). It is an extension of the logistic equation described in Box 5.4. Its virtues are (like the logistic) its simplicity, and its capacity to shed light on the factors that determine the outcome of a competitive interaction.

Within the logistic equation,

$$\frac{dN}{dt} = rN \frac{(K - N)}{K}$$

the particular term that models intraspecific competition is  $(K - N)/K$ . Within this term, the greater the value of  $N$  (the bigger the population), the greater is the strength of intraspecific competition. The basis of the Lotka–Volterra model is the replacement of this term by one that models both intra- and interspecific competition. In the model, we call the population size of the first species  $N_1$ , and that of a second species  $N_2$ . Their carrying capacities and intrinsic rates of increase are  $K_1$ ,  $K_2$ ,  $r_1$  and  $r_2$ .

By analogy with the logistic, we expect the *total* competitive effect on, say, species 1 (intra- and interspecific) to be greater the larger the values of  $N_1$  and  $N_2$ ; but we cannot just add them together, since the competitive effects of the two species on species 1 are unlikely to be the same. Suppose, though, that 10 individuals of species 2 have, between them, only the same competitive effect on species 1 as does a single individual of species 1. The total competitive effect on species 1 will then be equivalent to the effect of  $(N_1 + N_2 * 1/10)$  species 1 individuals. The constant (1/10 in the present case) is called a *competition coefficient* and is denoted by  $\alpha_{12}$  (alpha one two). Multiplying  $N_2$  by  $\alpha_{12}$  converts it to a number of  $N_1$  equivalents, and adding  $N_1$  and  $\alpha_{12}N_2$  together gives us the total competitive effect on species 1. (Note that  $\alpha_{12} < 1$  means that individuals of species 2 have less inhibitory effect on individuals of species 1 than individuals of species 1 have on others of their own species, and so on.)

The equation for species 1 can now be written:

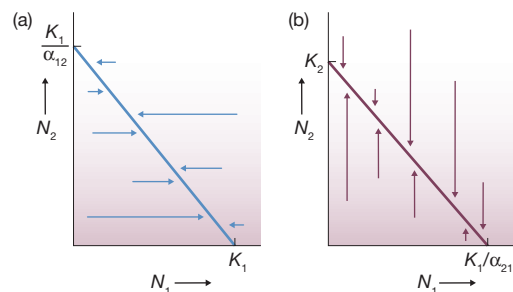
$$\frac{dN_1}{dt} = r_1 N_1 \frac{(K_1 - [N_1 + \alpha_{12}N_2])}{K_1}$$

and for species 2 (with its own competition coefficient, converting species 1 individuals into species 2 equivalents):

$$\frac{dN_2}{dt} = r_2 N_2 \frac{(K_2 - [N_2 + \alpha_{21}N_1])}{K_2}$$

These two equations constitute the Lotka–Volterra model.

The best way to appreciate its properties is to ask the question, ‘Under what circumstances does each species increase or decrease in abundance?’ In order to answer, it is necessary to construct diagrams in which all possible combinations of  $N_1$  and  $N_2$  can be displayed. This has been done in Figure 6.6. Certain combinations (certain regions in Figure 6.6) give rise to increases in species 1 and/or species 2, whereas other combinations give rise to decreases. It follows inevitably that there must also therefore be a so-called



**Figure 6.6**

The zero isoclines generated by the Lotka–Volterra competition equations. (a) The  $N_1$  zero isocline: species 1 increases below and to the left of it, and decreases above and to the right of it. (b) The equivalent  $N_2$  isocline.



zero isocline for each species: that is, a line with combinations leading to increase on one side of it and combinations leading to decrease on the other, but along which there is neither increase nor decrease.

We can map out the regions of increase and decrease in Figure 6.6 for species 1 if we can draw its zero isocline, and we can do this by using the fact that on the zero isocline,  $dN_1/dt = 0$  (the rate of change of species 1 abundance is zero, by definition). Rearranging the equation, this gives us, as the zero isocline for species 1:

$$N_1 = K_1 - \alpha_{21}N_2$$

Below and to the left of this, species 1 increases in abundance (arrows in the figure, representing this increase, point from left to right, since  $N_1$  is on the horizontal axis). It increases because numbers of both species are relatively low, and species 1 is thus subjected to only weak competition. Above and to the right of the line, however, numbers are high, competition is strong and species 1 decreases in abundance (arrows from right to left). Based on an equivalent derivation, Figure 6.6b also shows the species 2 zero isocline, with arrows, like the  $N_2$  axis, running vertically.

In order to determine the outcome of competition in this model, it is necessary to determine, at each point on a figure, the behavior of the joint species 1–species 2 population, as indicated by the pair of arrows. There are, in fact, four different ways in which the two zero isoclines can be arranged relative to one another, and these can be distinguished by the intercepts of the zero isoclines (Figure 6.7). The outcome of competition will be different in each case.

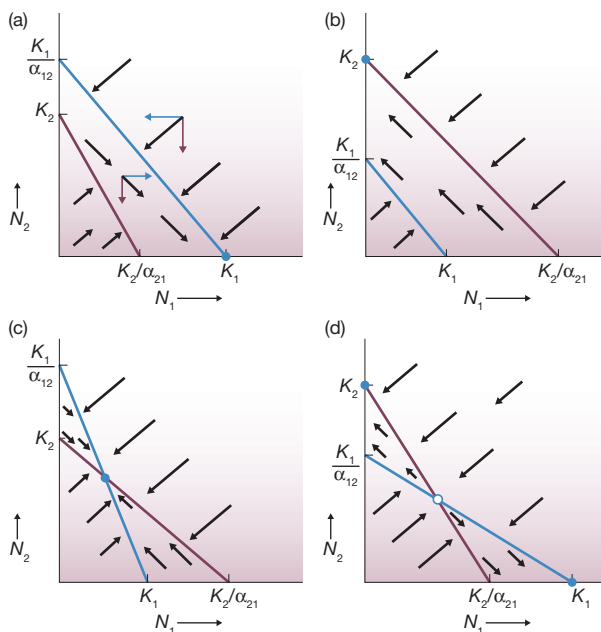
Looking at the intercepts in Figure 6.7a, for instance,

$$\frac{K_1}{\alpha_{12}} > K_2 \quad \text{and} \quad K_1 > \frac{K_2}{\alpha_{21}}$$

Rearranging these slightly gives us:

$$K_1 > K_2\alpha_{12} \quad \text{and} \quad K_1\alpha_{21} > K_2$$

The first inequality ( $K_1 > K_2\alpha_{12}$ ) indicates that the inhibitory intraspecific effects that species 1 can exert on itself (denoted by  $K_1$ ) are greater than the interspecific effects that species 2 can exert on species 1 ( $K_2\alpha_{12}$ ). This means that species 2 is a weak interspecific competitor. The second inequality, however, indicates that species 1 can exert more of an effect



**Figure 6.7**

The outcomes of competition generated by the Lotka–Volterra competition equations for the four possible arrangements of the  $N_1$  and  $N_2$  zero isoclines. Black arrows refer to joint populations, and are derived as indicated in (a). The solid circles show stable equilibrium points. The open circle in (d) is an unstable equilibrium point. For further discussion, see box text.

on species 2 than species 2 can on itself. Species 1 is thus a *strong* interspecific competitor; and as the arrows in Figure 6.7a show, species 1 drives the weak species 2 to extinction and attains its own carrying capacity. The situation is reversed in Figure 6.7b. Hence Figure 6.7a and b describe cases in which the environment is such that one species invariably outcompetes the other, because the first is a strong interspecific competitor and the other weak.

In Figure 6.7c, by contrast:

$$K_1 > K_2\alpha_{12} \quad \text{and} \quad K_2 > K_1\alpha_{21}$$

In this case, both species have less competitive effect on the other species than those other species have on themselves; in this sense, both are weak competitors. This would happen, for example, if there were niche differentiation between the species – each competed mostly ‘within’ its own niche. The outcome, as Figure 6.7c shows, is that all arrows point towards a stable, equilibrium combination of the two species, which all joint populations therefore tend to approach: that is, the outcome of this type of competition is the stable coexistence of the competitors. Indeed, it is only this type of competition (both species having more effect on themselves than on the other

species) that does lead to the stable coexistence of competitors.

Finally, in Figure 6.7d:

$$K_2\alpha_{12} > K_1 \quad \text{and} \quad K_1\alpha_{21} > K_2$$

Thus individuals of both species have a greater competitive effect on individuals of the other species than those other species do on themselves. This will occur, for instance, when each species is more aggressive toward individuals of the other species than toward individuals of its own species. The directions of the arrows are rather more complicated in this case, but eventually they always lead to one or other of two alternative stable points. At the first, species 1 reaches its carrying capacity with species 2 extinct; at the second, species 2 reaches its carrying capacity with species 1 extinct. In other words, both species are capable of driving the other species to extinction, but which actually does so cannot be predicted with certainty. It depends on which species has the upper hand in terms of densities, either because they start with a higher density or because density fluctuations in some other way give them that advantage. Whichever species has this upper hand, capitalizes on that and drives the other species to extinction.

does not prove that there are coexisting competitors. The species may not be competing at all and may never have done so in their evolutionary history. We require proof of interspecific competition. In the examples above, this was provided by experimental manipulation – remove one species (or one group of species) and the other species increases its abundance or its survival. But most of even the more plausible cases for competitors coexisting as a result of niche differentiation have not been subjected to experimental proof. So just how important is the Competitive Exclusion Principle in practice? We return to this question in Section 6.5.

Part of the problem is that although species may not be competing now, their ancestors may have competed in the past, so that the mark of interspecific competition is left imprinted on the niches, the behavior or the morphology of their present-day descendants. This particular question is taken up in Section 6.3.

Finally, the Competitive Exclusion Principle, as stated above, includes the word ‘stable’. That is, in the habitats envisaged in the principle, conditions and the supply of resources remain more or less constant – if species compete, then that competition runs its course, either until one of the species is eliminated or until the species settle into a pattern of coexistence within their realized niches. Sometimes this is a realistic view of a habitat, especially in laboratory

or other controlled environments where the experimenter holds conditions and the supply of resources constant. However, most environments are not stable for long periods of time. How does the outcome of competition change when environmental heterogeneity in space and time are taken into consideration? This is the subject of the next section.

### 6.2.8 Environmental heterogeneity

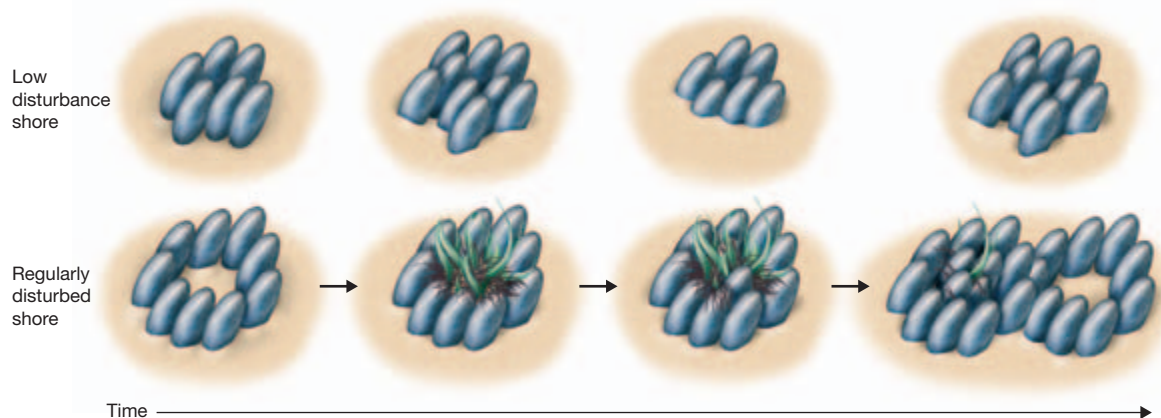
As explained in previous chapters, spatial and temporal variations in environments are the norm rather than the exception. Environments are usually a patchwork of favorable and unfavorable habitats; patches are often only available temporarily; and patches often appear at unpredictable times and in unpredictable places. Under such variable conditions, competition may only rarely ‘run its course’, and the outcome cannot be predicted simply by application of the Competitive Exclusion Principle. A species that is a ‘weak’ competitor in a constant environment might, for example, be good at colonizing open gaps created in a habitat by fire, or a storm, or the hoofprint of a cow in the mud – or may be good at growing rapidly in such gaps immediately after they are colonized. It may then coexist with a strong competitor, as long as new gaps occur frequently enough. Thus, a realistic view of interspecific competition must acknowledge that it often proceeds not in isolation, but under the influence of, and within the constraints of, a patchy, impermanent or unpredictable world.

The following examples illustrate just two of the many ways in which environmental heterogeneity ensures that the Competitive Exclusion Principle is very far from being the whole story when it comes to determining the outcome of an interaction between competing species.

The first concerns the coexistence of a superior competitor and a superior colonizer: the sea palm *Postelsia palmaeformis* (a brown alga) and the mussel *Mytilus californianus* on the coast of Washington, USA (Paine, 1979) (Figure 6.8).

competition may only rarely  
‘run its course’

mussels, sea palms and the  
frequency of gap formation



**Figure 6.8**

On shores in which gaps are not created, mussels are able to exclude the brown alga *Postelsia*; but where gaps are created regularly enough the two species coexist, even though *Postelsia* is eventually excluded by the mussels from each gap.

Seashore with *Postelsia*  
and *Mytilus californianus*.



© GERALD AND BUFF CORSI, VISUALS UNLIMITED

*Postelsia* is an annual plant that must re-establish itself each year in order to persist at a site. It does so by attaching to the bare rock, usually in gaps in the mussel bed created by wave action. However, the mussels themselves slowly encroach on these gaps, gradually filling them and precluding colonization by *Postelsia*. In other words, in a stable environment, the mussels would outcompete and exclude *Postelsia*. But their environment is not stable – gaps are frequently being created. It turns out that these species coexist only at sites in which there is a relatively high average rate of gap formation (at least 7% of surface area per year), and in which this rate is approximately the same each year. Where the average rate is lower, or where it varies considerably from year to year, there is (either regularly or occasionally) a lack of bare rock for colonization by *Postelsia*. At the sites of coexistence, on the other hand, although *Postelsia* is eventually excluded from each gap, these are created with sufficient frequency and regularity for there to be coexistence in the site as a whole. In short, there is coexistence of competitors – but not as a result of niche differentiation.

coexistence as a result of  
aggregated distributions

A perhaps more widespread path to the coexistence of a superior and an inferior competitor is based on the idea that the two species may have independent, aggregated (i.e. clumped) distributions over the available habitat. This would mean that the powers of the superior competitor were mostly directed against members of its own species (in the high-density clumps), but that this aggregated superior competitor would be absent from many areas – within which the inferior competitor could escape competition. An inferior competitor may then be able to coexist with a superior competitor that would rapidly exclude it from a continuous, homogeneous environment.

That such aggregated distributions are indeed a reality is illustrated by a field study of two species of sand-dune plant, *Aira praecox* and *Erodium cicutarium*, in northwest England. Both species were aggregated, and the smaller plant, *Aira*, tended to be aggregated even at the smallest spatial scales (Figure 6.9a). The two species, though, were negatively associated with one another at these smallest scales (Figure 6.9b). Thus, *Aira* tended to occur in small single-species clumps and was therefore much less liable to competition from *Erodium* than would have been the case if they had been distributed at random.

The consequences of such aggregated distributions are illustrated by a study of experimental communities of four annual terrestrial plants – *Capsella*

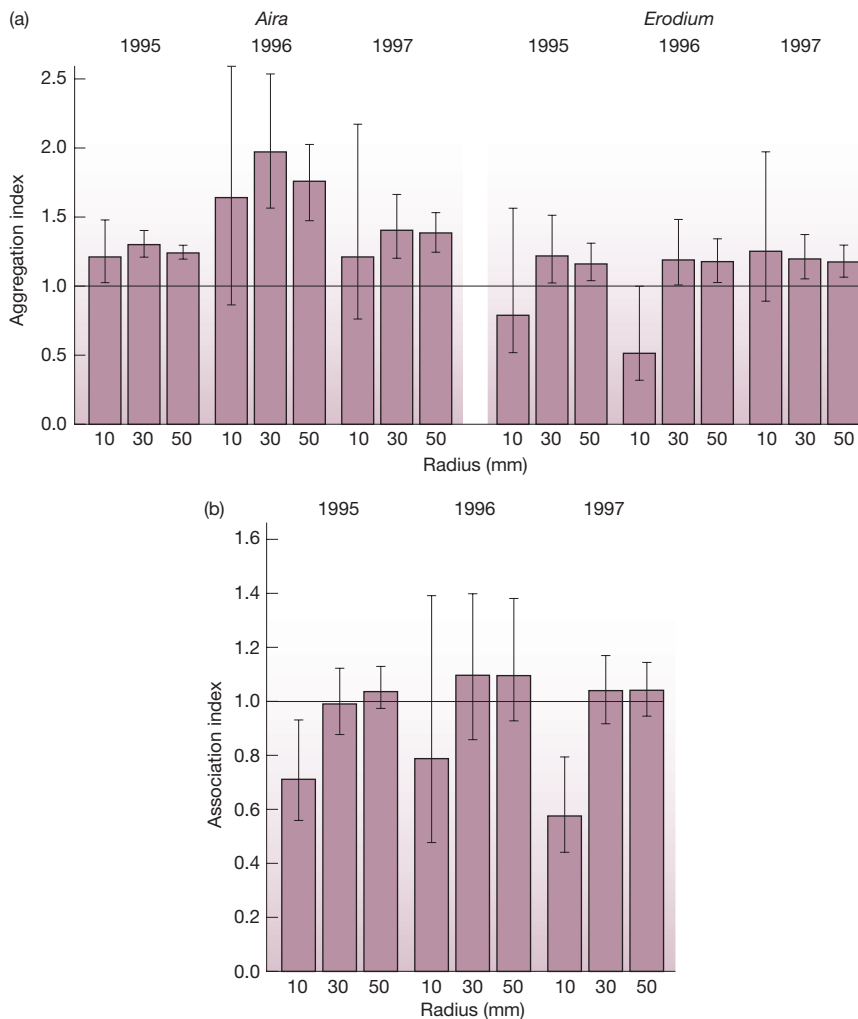


Figure 6.9

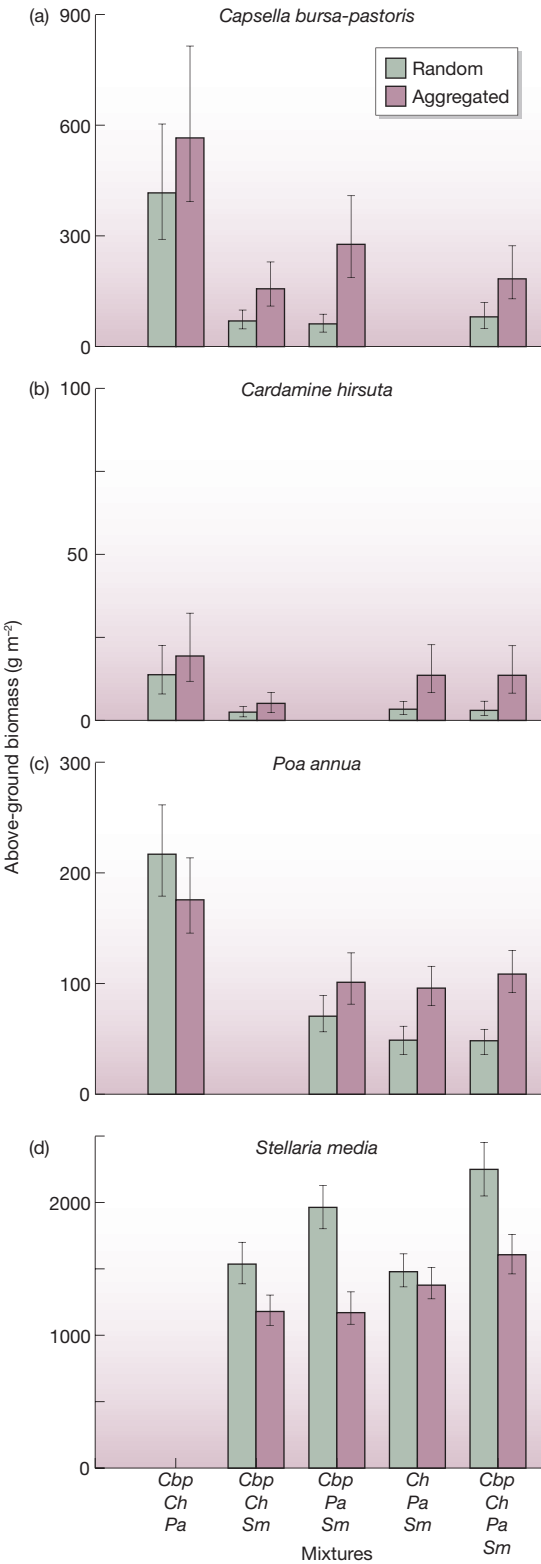
(a) Spatial distribution of two sand-dune species, *Aira praecox* and *Erodium cicutarium* at a site in northwest England. An aggregation index of 1 indicates a random distribution. Indices greater than 1 indicate aggregation (clumping) within patches with the radius as specified; values less than 1 indicate a regular distribution. Bars represent 95% confidence intervals. (b) The association between *Aira* and *Erodium* in each of the 3 years. An association index greater than 1 would indicate that the two species tended to be found together more than would be expected by chance alone in patches with the radius as specified; values less than 1 indicate a tendency to find one species or the other. Bars represent 95% confidence intervals.

*bursa-pastoris*, *Cardamine hirsuta*, *Poa annua* and *Stellaria media* (Figure 6.10). *Stellaria* is known to be the superior competitor among these species. Replicate three- and four-species mixtures were sown at high density, and the seeds were either placed completely at random, or seeds of each species were aggregated in subplots within the experimental areas. Intraspecific aggregation harmed the performance of the superior *Stellaria* in the mixtures, whereas in all but one case aggregation improved the performance of the three inferior competitors. Again, coexistence of competitors was favored not by niche differentiation but simply by a type of heterogeneity that is typical of the natural world: aggregation ensured that most individuals competed with members of their own and not of another species.

These studies, and others like them, go a long way toward explaining the co-occurrence of species that in constant, homogeneous environments would probably exclude one another. The environment is rarely unvarying enough for competitive exclusion to run its course or for the outcome to be the same across the landscape.

Figure 6.10

The effect of intraspecific aggregation on above-ground biomass (mean  $\pm$  SE) of four plant species grown for 6 weeks in three- and four-species mixtures (four replicates of each). The normally competitively superior *Stellaria media* (*Sm*) did consistently less well when seeds were aggregated than when they were placed at random (d). In contrast, the three competitively inferior species – *Capsella bursa-pastoris* (*Cbp*), *Cardamine hirsuta* (*Ch*) and *Poa annua* (*Pa*) – almost always performed better when seeds had been aggregated (a–c). Note the different scales on the vertical axes, and that the compositions of the mixtures are given only along the horizontal axis of (d).





## 6.3 Evolutionary effects of interspecific competition

Putting to one side the fact that environmental heterogeneity ensures that the forces of interspecific competition are often much less profound than they would otherwise be, it is nonetheless the case that the potential of interspecific competition to adversely affect individuals is considerable. We have seen in Chapter 2 that natural selection in the past will have favored those individuals that, by their behavior, physiology or morphology, have avoided adverse effects that act on other individuals in the same population. The adverse effects of extreme cold, for example, may have favored individuals with an enzyme capable of functioning effectively at low temperatures. Similarly, in the present context, the adverse effects of interspecific competition may have favored those individuals that managed to avoid those competitive effects. We can, therefore, expect species to have evolved characteristics that ensure that they compete less, or not at all, with members of other species.

How will this look to us at the present time? Coexisting species, with an apparent potential to compete, will exhibit differences in behavior, physiology or morphology that ensure that they compete little or not at all. Connell has called this line of reasoning ‘invoking the ghost of competition past’. Yet the pattern it predicts is precisely the same as that supposed by the Competitive Exclusion Principle to be a prerequisite for the coexistence of species that still compete. Coexisting present-day competitors, and coexisting species that have evolved an avoidance of competition, can look the same.

The question of how important either past or present competition are as forces structuring natural communities will be addressed in the last section of this chapter (Section 6.5). For now, we examine some examples of what interspecific competition *can* do as an evolutionary force. Note, however, that by invoking something that cannot be observed directly (evolution), it may be impossible to prove an evolutionary effect of interspecific competition, in the strict sense of ‘proof’ that can be applied to mathematical theorems or carefully controlled experiments in the laboratory. Nonetheless, we consider some examples where an evolutionary (rather than an ecological) effect of interspecific competition is the most reasonable explanation for what is observed.

evolutionary avoidance of competition

invoking the ghost of competition past

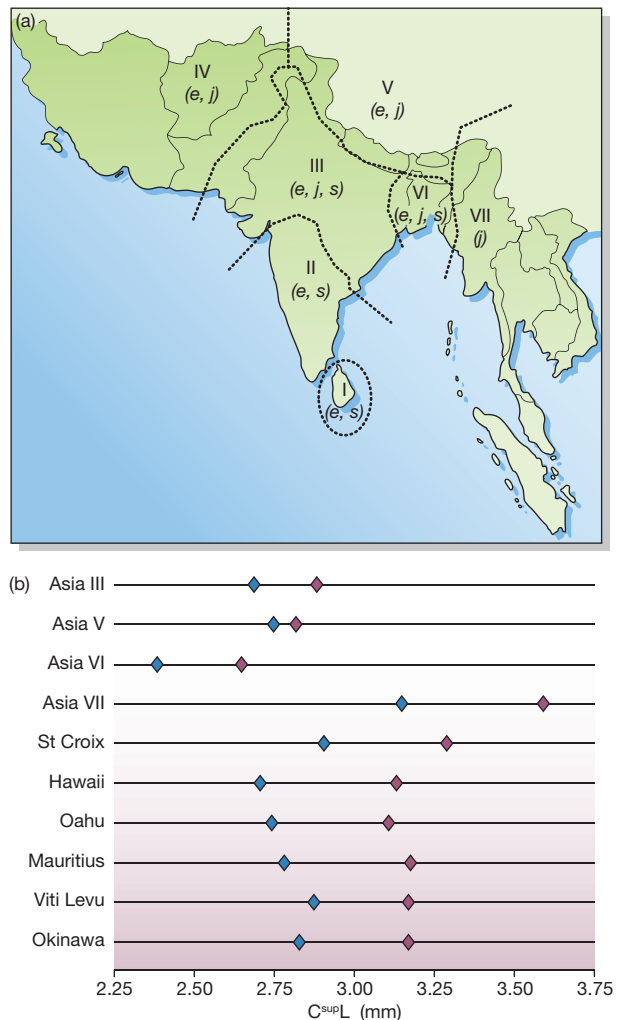
the difficulty of distinguishing ecological and evolutionary effects

### 6.3.1 Character displacement and ecological release in the Indian mongoose

In western parts of its range, the small Indian mongoose (*Herpestes javanicus*) coexists with one or two slightly larger species in the same genus (*H. edwardsii* and *H. smithii*), but these species are absent in the eastern part of its range (Figure 6.11a). The upper canine teeth are the mongoose’s principal prey-killing organ, and these vary in size within and between species and between the sexes (female mongooses are smaller than males). In the east, where *H. javanicus* occurs alone (area VII in Figure 6.11a), both males and females have larger canines than in the western areas (III, V, VI) where it coexists with the larger species (Figure 6.11b). This is consistent with the view that where similar but larger mongoose species are present, the prey-catching apparatus of *H. javanicus* has

Figure 6.11

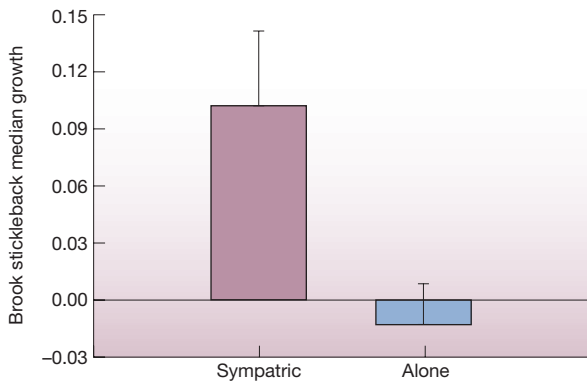
(a) Native geographic ranges of *Herpestes javanicus* (*j*), *H. edwardsii* (*e*) and *H. smithii* (*s*). (b) Maximum diameter (mm) of the upper canine ( $C^{\text{supL}}$ ) for *Herpestes javanicus* in its native range [data only for areas III, V, VI and VII from (a)] and islands on which it has been introduced. Symbols in blue represent mean female size and in maroon mean male size. Compared to area VII (*H. javanicus* alone), animals in areas III, V and VI, where they compete with the two larger species, are smaller. On the islands, they have increased in size since their introduction, but are still not as large as in area VII.



smaller teeth in the small Indian mongoose when larger competitors are present

been selected for reduced size (referred to as ‘character displacement’), reducing the strength of competition with other species in the genus because smaller predators tend to take smaller prey. Where *H. javanicus* occurs in isolation, since no character displacement has occurred, its canine teeth are much larger. (Another strong candidate for the evolutionary effects of interspecific competition, especially because of its association with character displacement, is provided by Darwin’s finches of the genus *Geospiza* living on the Galapagos islands, discussed in Section 2.4.2.)

In fact, *H. javanicus* was introduced about a century ago to many islands outside its native range (often as part of a naive attempt to control introduced rodents). In these places, the larger competitor mongoose species were absent. Within 100–200 generations *H. javanicus* had increased in size (Figure 6.11b), so that the sizes of island individuals are now intermediate between those in the region of origin (where they coexisted with other species and were small) and those in the east where they occur alone. Their size on the islands is consistent with ‘ecological release’ from competition with larger species.

**Figure 6.12**

Means (with standard errors) of group median growth (natural log of the final mass of fish in each enclosure divided by the initial mass of the group) for sympatric brook sticklebacks, representing post-displacement phenotypes (maroon bar), and brook sticklebacks living alone, representing pre-displacement phenotypes (blue bar), both reared in the presence of ninespine sticklebacks. In competition with ninespine sticklebacks, growth was significantly greater for post-displacement vs pre-displacement phenotypes ( $P = 0.012$ ).

### 6.3.2 Character displacement in Canadian sticklebacks

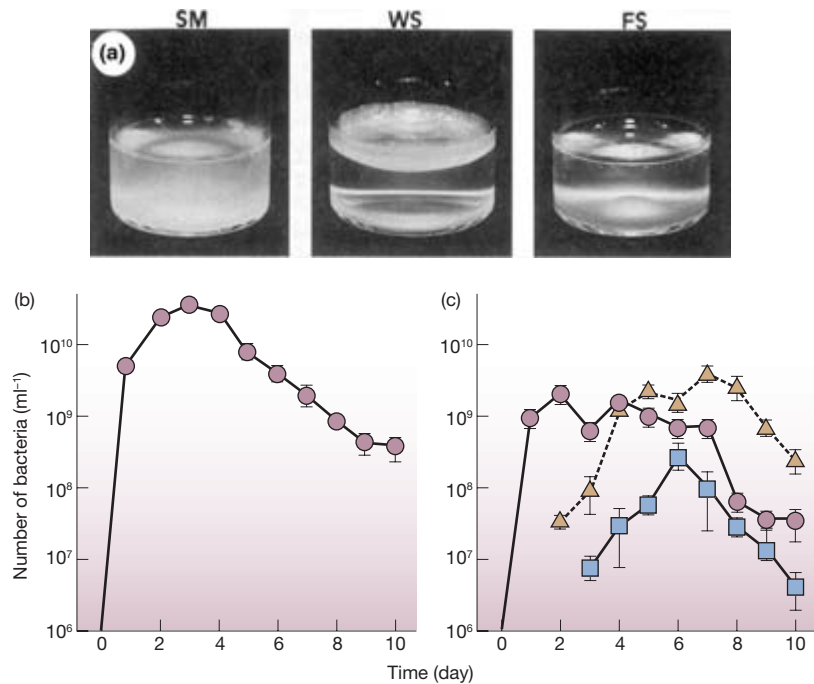
If character displacement has ultimately been caused by competition, then the effects of competition should decline with the degree of displacement. Brook sticklebacks, *Culaea inconstans*, coexist in some Canadian lakes with ninespine sticklebacks, *Pungitius pungitius* (the species are ‘sympatric’), whereas in other lakes brook sticklebacks live alone. In sympatry, the brook sticklebacks possess significantly shorter gill rakers (more suited for foraging in open water), longer jaws and deeper bodies. We can consider the brook sticklebacks living alone as having pre-displacement morphology and the sympatric brook sticklebacks as post-displacement phenotypes. When each phenotype was placed separately in enclosures in the presence of ninespine sticklebacks, the pre-displacement brook sticklebacks grew significantly less well than their sympatric post-displacement counterparts (Figure 6.12). This is clearly consistent with the hypothesis that the post-displacement phenotype has evolved to avoid competition, and hence enhance fitness, in the presence of ninespine sticklebacks.

### 6.3.3 Evolution in action: niche-differentiated bacteria

The most direct way of demonstrating the evolutionary effects of competition within a pair of competing species is for the experimenter to induce these effects – impose the selection pressure (competition) and observe the outcome. Surprisingly perhaps, there have been very few successful experiments of this type. To find an example of niche differentiation giving rise to coexistence of competitors in a selection experiment, we must turn away from interspecific competition in the strictest sense to competition between three types of the same bacterial species, *Pseudomonas fluorescens*, which behave as separate species because they reproduce asexually. The three types are named ‘smooth’ (SM), ‘wrinkly spreader’ (WS) and ‘fuzzy spreader’ (FS), on the basis of the morphology of their colonies plated out on solid medium. In liquid medium they also occupy quite different parts of the culture vessel (Figure 6.13a), that is, they have separate niches. In vessels that were continually shaken, so that no separate niches could be established, an initially pure culture of SM individuals retained its purity (Figure 6.13b). But in the absence of shaking, WS and FS mutants arose in the SM population, increased in frequency and established themselves (Figure 6.13c): evolution had favored niche differentiation and the consequent avoidance of competition.

**Figure 6.13**

(a) Pure cultures of three types of the bacterium *Pseudomonas fluorescens* (smooth, SM; wrinkly spreader, WS; fuzzy spreader, FS) concentrate their growth in different parts of a liquid culture vessel. (b) In shaken culture vessels, pure SM cultures are maintained. Bars are standard errors. (c) But in unshaken, initially pure SM (●) cultures, WS (▲) and FS (■) mutants arise, invade and establish. Bars are standard errors.



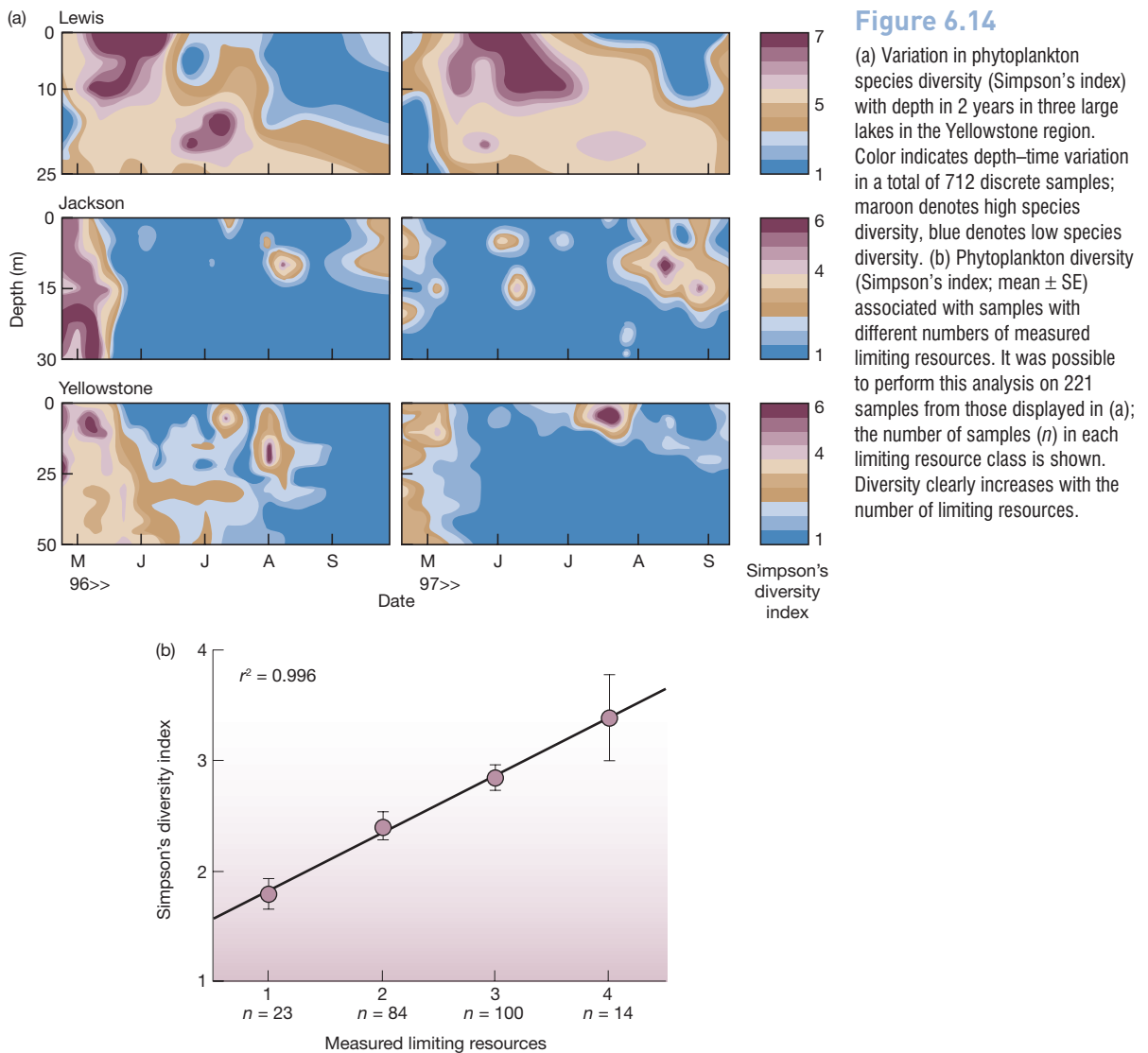
AFTER RAINEY &amp; TREVISANO, 1998, BY PERMISSION OF NATURE

## 6.4 Interspecific competition and community structure

Interspecific competition, then, has the potential to either keep apart (Section 6.2) or drive apart (Section 6.3) the niches of coexisting competitors. How can these forces express themselves when it comes to the role of interspecific competition in molding the shape of whole ecological communities – who lives where and with whom?

### 6.4.1 Limiting resources and the regulation of diversity in phytoplankton communities

We begin by returning to the question of coexistence of competing phytoplankton species. In Section 6.2.4, we saw how two diatom species could coexist in the laboratory on two shared limiting resources – silicate and phosphate. In fact, theory predicts that the diversity of coexisting species should be proportional to the number of resources in a system that are at physiological limiting levels (Tilman, 1982): the more limiting resources, the more coexisting competitors. A direct test of this hypothesis examined three lakes in the Yellowstone region of Wyoming, USA using an index (Simpson's index) of the species diversity of phytoplankton there (diatoms and other species). If one species exists on its own, the index equals 1; in a group of species where biomass is strongly dominated by a single species, the index will be close to 1; when two species exist at equal biomass, the index is 2; and so on. According to the theory, therefore, this index



should increase in direct proportion to the number of resources limiting growth. The spatial and temporal patterns in phytoplankton diversity in the three lakes for 1996 and 1997 are shown in Figure 6.14a.

The principal limiting resources for phytoplankton growth are nitrogen, phosphorus, silicon and light. These parameters were measured at the same depths and times that the phytoplankton were sampled, and it was noted where and when any of the potential limiting factors actually occurred at levels below threshold limits for growth. Consistent with the theory, species diversity increased as the number of resources at physiologically limiting levels increased (Figure 6.14b). This suggests that even in the highly dynamic environments of lakes, where equilibrium conditions are rare, resource competition plays a role in continuously structuring the phytoplankton community. It is heartening that the results

as predicted, highest phytoplankton diversity occurred where many resources were limiting

of experiments performed in the artificial world of the laboratory (Section 6.2.4) are echoed here in the much more complex natural environment.

### 6.4.2 Niche complementarity amongst anemone fish in Papua New Guinea

In another study of niche differentiation and coexistence, a number of species of anemone fish were examined near Madang in Papua New Guinea. This region has the highest reported species richness of both anemone fish (nine) and their host anemones (10). Each individual anemone tends to be occupied by individuals of just one species of anemone fish, because the residents aggressively exclude intruders. However, aggressive interactions were less frequently observed between anemone fish of very different sizes. Anemones seem to be a limiting resource for the fish in that almost all anemones were occupied, and when some were transplanted to new sites they were quickly colonized. Surveys in four zones (nearshore, mid-lagoon, outer barrier reef and offshore: Figure 6.15a) showed that each anemone fish was primarily associated with a particular species of anemone; each also showed a characteristic preference for a particular zone (Figure 6.15b). Crucially, moreover, anemone fish that lived with the same anemone were typically associated with different zones. For example, *Amphiprion percula* occupied the anemone *Heteractis magnifica* in nearshore zones, while *A. perideraion* occupied *H. magnifica* in offshore zones. Finally, associated with the lowered level of aggression, small anemone fish species (*A. sandaracinos* and *A. leucokranos*) were able to cohabit the same anemone with larger species.

species similar in one dimension  
tend to differ in another  
dimension

Two important points are illustrated here. First, the anemone fish demonstrate *niche complementarity*; that is, niche differentiation involves several niche dimensions: species of anemone, zone on the shore and, almost certainly, some other dimension, perhaps food particle size, reflected in the size of the fish. Fish species that occupy a similar position along one dimension tend to differ along another dimension. Second, the fish can be considered to be a guild, in that they are a group of species that exploit the same class of environmental resource in a similar way, and insofar as interspecific competition plays a role in structuring communities, it tends to do so, as here, not by affecting some random sample of the members of that community, nor by affecting every member, but by acting within guilds.

### 6.4.3 Species separated in space or in time

In spite of the many examples where there is no direct connection between interspecific competition and niche differentiation, there is no doubt that niche differentiation is often the basis for the coexistence of species within natural communities. There are a number of ways in which niches can be differentiated. One, as we have seen, is resource partitioning or differential resource utilization. This can be observed when species living in precisely the same habitat nevertheless utilize different resources. In many cases, however, the resources used by ecologically similar species are separated spatially. Differential resource utilization will then express itself as either a microhabitat differentiation between the species (different species of fish, say, feeding at different depths) or even a difference in



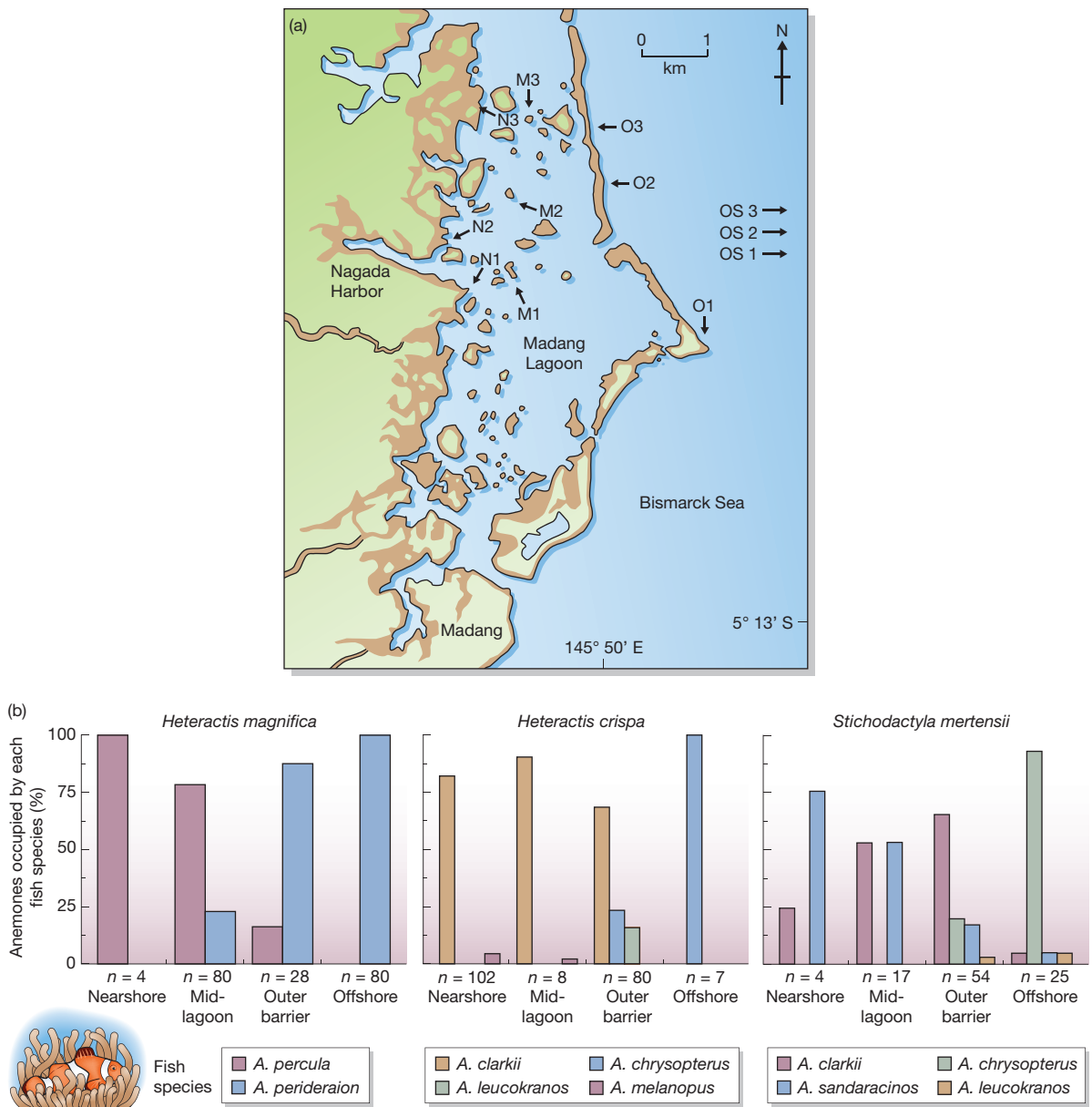


Figure 6.15

(a) Map showing the location of three replicate study sites in each of four zones within and outside Madang Lagoon (N, nearshore; M, mid-lagoon; O, outer barrier reef; OS, offshore reef). The blue areas indicate water, brown shading represents coral reef, and green represents land.

(b) The percentage of three common species of anemone (*Heteractis magnifica*, *H. crispa* and *Stichodactyla mertensii*) occupied by different anemone fish species (*Amphiprion* spp., in key below) in each of the four zones. The number of anemones censused in each zone is shown by *n*.

geographic distribution. Alternatively, the availability of the different resources may be separated in time; that is, different resources may become available at different times of the day or in different seasons. Differential resource utilization may then express itself as a temporal separation between the species.

The other major way in which niches can be differentiated is on the basis of conditions. Two species may use precisely the same resources, but if their ability to do so is influenced by environmental conditions (as it is bound to be), and if they respond differently to those conditions, then each may be competitively superior in different environments. This too can express itself as either a microhabitat differentiation, or a difference in geographic distribution, or a temporal separation, depending on whether the appropriate conditions vary on a small spatial scale, a large spatial scale or over time. Of course, it is not always easy to distinguish between conditions and resources, especially with plants (see Chapter 3). Niches may then be differentiated on the basis of a factor (such as water), which is both a resource and a condition.

#### 6.4.4 Spatial separation in trees and tree-root fungi

trees in Borneo: height, depth, gaps and soil

Trees vary in their capacity to use resources such as light, water and nutrients. A study in Borneo of 11 tree species in the genus *Macaranga* showed marked differentiation in light requirements, from extremely light-demanding species such as *M. gigantea* to shade-tolerant species such as *M. kingii* (Figure 6.16a). Average light levels intercepted by the crowns of trees tended to increase as they grew larger, but the ranking of the species did not change. The shade-tolerant species were smaller (Figure 6.16b) and persisted in the understorey, rarely establishing in disturbed microsites (e.g. *M. kingii*), in contrast to some of the larger, high-light species that are pioneers of large forest gaps (e.g. *M. gigantea*). Others were associated with intermediate light levels and can be considered small-gap specialists (e.g. *M. trachyphylla*). The *Macaranga* species were also differentiated along a second niche gradient, with some species being more common on clay-rich soils and others on sand-rich soils (Figure 6.16b). This differentiation may be based on nutrient availability (generally higher in clay soils) and/or soil moisture availability (possibly lower in the clay soils because of thinner root mats and humus layers). Hence, as with the anemone fish, there is evidence of niche complementarity: species with similar light requirements tended to differ in terms of preferred soil textures. In addition, though, the apparent niche partitioning by *Macaranga* species was partly related to space horizontally (variation in soil types and in light levels from place to place) and partly to space vertically (height in the canopy, depth of the root mat).

separation with depth in ectomycorrhizal fungi

Differential resource utilization in the vertical plane has also been demonstrated for fungi intimately associated with plant roots (ectomycorrhizal fungi; see Section 8.4.5) in the floor of a forest of pine, *Pinus resinosa* (Figure 6.17). Until recently, it was not possible to study the distribution of ectomycorrhizal species in their natural environment. Now DNA analyses make this possible and allow their distributions to be compared. The forest soil has a well-developed litter layer above a fermentation layer (F layer) and a thin humified layer (H layer), with mineral soil beneath (B horizon). Of the 26 species separated by the DNA analysis, some were very largely restricted to the litter layer (group A in Figure 6.17), others to the F layer (group D), the H layer (group E) or the B horizon (group F). The remaining species were more general in their distributions (groups B and C). This is therefore an example of where a spatial (microhabitat) separation cannot simply be ascribed to one resource or condition: there are no doubt several that vary with the soil layers.

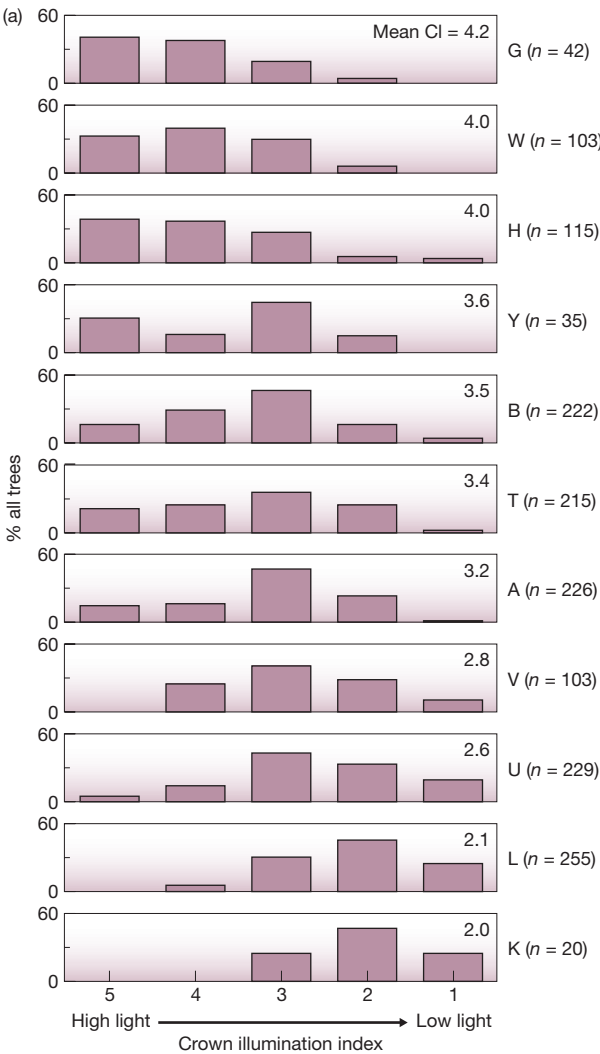


Figure 6.16

(a) Percentage of individuals in each of five crown illumination (CI) classes for 11 *Macaranga* species (sample sizes in parentheses). (b) Three-dimensional distribution of the 11 species with respect to maximum height, the proportion of stems in high light levels [class 5 in (a)] and proportion of stems in sand-rich soils. Each species of *Macaranga* is denoted by a single letter. G, *gigantea*; W, *winkleri*; H, *hosei*; Y, *hypoleuca*; B, *beccariana*; T, *triloba*; A, *trachyphylla*; V, *havilandii*; U, *hullettii*; L, *lamellata*; K, *kingii*.

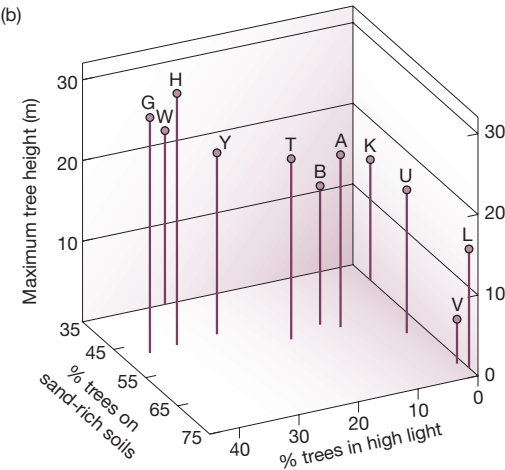
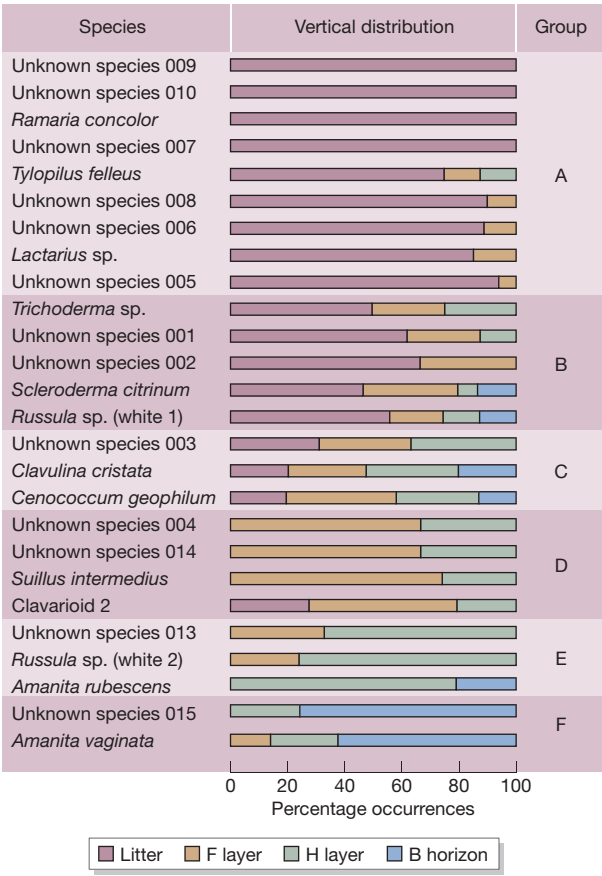


Figure 6.17

The vertical distribution of 26 ectomycorrhizal fungal species in the floor of a pine forest determined by DNA analysis. Most have not formally been named but are shown as a code. Vertical distribution histograms show the percentage of occurrences of each species in the litter (maroon), F layer (yellow), H layer (green) and B horizon (blue).



AFTER DICKIE ET AL., 2002

6.4.5 Temporal separation in mantids and tundra plants

staggered life cycles in mantids

One common way in which resources may be partitioned over time is through a staggering of life cycles through the year. It is notable that two species of mantids, which feature as predators in many parts of the world, commonly coexist both in Asia and North America. *Tenodera sinensis* and *Mantis religiosa* have life cycles that are 2–3 weeks out of phase. To test the hypothesis that this asynchrony serves to reduce interspecific competition, the timing of their egg hatch was experimentally synchronized in replicated field enclosures (Hurd & Eisenberg, 1990). *T. sinensis*, which normally hatches earlier, was unaffected by *M. religiosa*. In contrast, the survival and body size of *M. religiosa* declined in the presence of *T. sinensis*. Because these mantids are both competitors for shared resources and predators of each other, the outcome of this experiment probably reflects a complex interaction between the two processes.

nitrogen, depth and time in Alaskan plants

In plants too, resources may be partitioned in time. Thus, tundra plants growing in nitrogen-limited conditions in Alaska are differentiated in their timing of nitrogen uptake, as well as the soil depth from which it is extracted and the

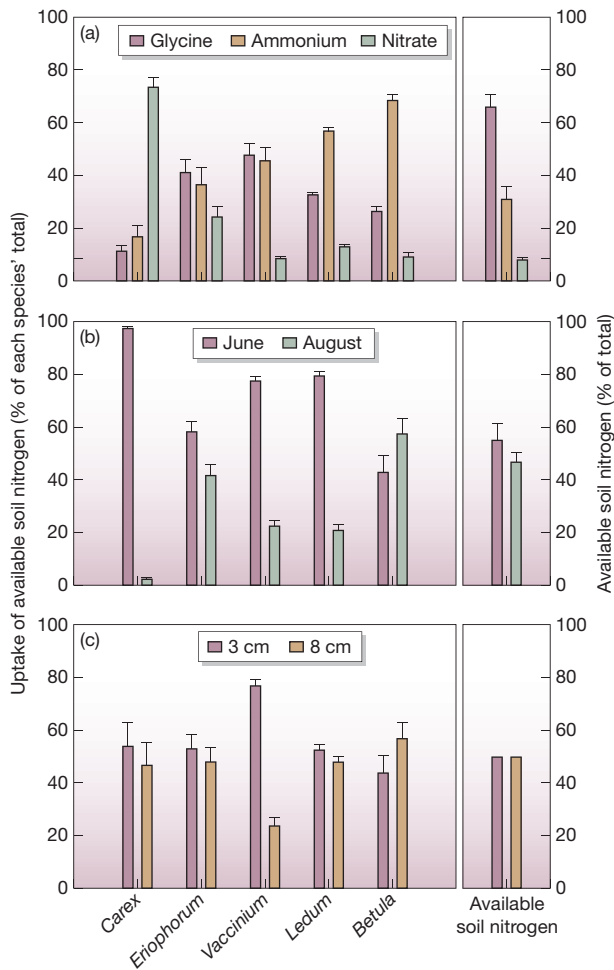


Figure 6.18

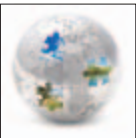
Mean uptake of available soil nitrogen ( $\pm$  SE) in terms of (a) chemical form, (b) timing of uptake and (c) depth of uptake by the five most common species in tussock tundra in Alaska. Data are expressed as the percentage of each species' total uptake (left panels) or as the percentage of the total pool of nitrogen available in the soil (right panels).

AFTER MCKANE ET AL., 2002

chemical form of nitrogen used. To trace how tundra species differed in uptake of different nitrogen sources, McKane et al. (2002) injected three chemical forms labeled with the rare isotope  $^{15}\text{N}$  (ammonium, nitrate and glycine) at two soil depths (3 and 8 cm) on two occasions (June 24 and August 7). Concentration of the  $^{15}\text{N}$  tracer was measured in each of five common tundra plants 7 days after application. The five plants proved to be well differentiated in their use of nitrogen sources (Figure 6.18). Cottongrass (*Eriophorum vaginatum*) and the cranberry bush (*Vaccinium vitis-idaea*) both relied on a combination of glycine and ammonium, but cranberry obtained more of these forms early in the growing season and at a shallower depth than cottongrass. The evergreen shrub *Ledum palustre* and the dwarf birch (*Betula nana*) used mainly ammonium, but *L. palustre* obtained more of this form early in the season while the birch exploited it later. Finally, the grass *Carex bigelowii* was the only species to use mainly nitrate. Here, niche complementarity can be seen along three niche dimensions: nitrogen source, depth and time.

## 6.5 How significant is interspecific competition in practice?

Competitors may exclude one another, or they may coexist if there is ecologically significant differentiation of their realized niches (Section 6.2). On the other hand, interspecific competition may exert neither of these effects if environmental heterogeneity prevents the process from running its course (Section 6.2.8). Evolution may drive the niches of competitors apart until they coexist but no longer compete (Section 6.3). All these forces may express themselves at the level of the ecological community (Section 6.4). Interspecific competition sometimes makes a high profile appearance by having a direct impact on human activity (Box 6.2). In this sense, competition can certainly be of practical significance.



## 6.2 TOPICAL ECOncerns

### 6.2 Topical ECOncerns

#### Competition in action

When exotic plant species are introduced to a new environment, by accident or on purpose, they sometimes prove to be exceedingly good competitors and many native species suffer harmful consequences as a result. Some of them have even more far-reaching consequences for native ecosystems. This newspaper article by Beth Daley, published in the *Contra Costa Times* on June 27, 2001, concerns grasses that have invaded the Mojave Desert in the southern United States. Not only are the invaders outcompeting native wild flowers, they have also dramatically changed the fire regime.

##### Invader grasses endanger desert by spreading fire

The newcomers crowd out native plants and provide fuel for once-rare flames to damage the delicate ecosystem.

Charred creosote bushes dot a mesa in the Mojave Desert, the ruins of what was likely the first fire in the area in more than 1000 years.

Though deserts are hot and dry, they aren't normally much of a fire hazard because the vegetation is so sparse there isn't much to burn or any way for blazes to spread.

But, underneath these blackened creosote branches, the cause of the fire seven years ago has already grown back: flammable grasses fill the empty spaces between the native bushes, creating a fuse for the fire to spread again.

Tens of thousands of acres in the Mojave and other southwestern deserts have burned in the last decade, fueled by the red brome, cheat grass and Sahara mustard, tiny grasses and plants that grow back faster than any native species and shouldn't be there in the first place.

... The grasses brought to America from Eurasia more than a century ago have no natural enemies, and little can stop their spread across empty desert pavement. And, once an area is cleared of native vegetation by one or repeated fires, the grasses grow in even thicker, sometimes outcompeting native wildflowers and shrubs.

... 'These grasses could change the entire makeup of the Mojave Desert in short order', said William Schlesinger of Duke University, who has studied the Mojave Desert for more than 25 years. When he began his research in the 1970s, the grasses were in the Mojave, but there still



were vast areas left untouched. Now, he said, the grasses are virtually everywhere and soon will be in concentrations large enough to fuel massive fires. 'This is not an easy problem to solve', he said.

... Despite the harsh conditions, a rainbow of wildflowers blooms regularly in the desert, sometimes carpeting the ground with blossoms after a rainstorm. Zebra-tailed lizards, rattlesnakes, desert tortoises and kangaroo rats are able to get by for long periods without water and bear up under the sun. But the innocuous-looking grasses threaten all these species by choking out wildflowers and killing off shelter and food that they rely on.

... Esque [of the US Geological Survey] has roped off 12 experimental sites, six of which he burned in 1999 to see how quickly invasive species re-establish themselves. But the result only showed the unpredictability of the desert:

the first year, the invasive red brome took hold, but this year, native wildflowers came back in force.

... Esque said 'It's not black and white with what is going on. We don't know if we are looking at coexistence or competition.'

(All content © 2001 *Contra Costa Times* (Walnut Creek, CA) and may not be republished without permission.)

- 1 *Some people have suggested bringing sheep into the desert to graze the invading grasses. Do you think this is a sensible idea? What further information would help you make a decision?*
- 2 *The US Geological Survey scientist found that red brome grass appeared to be outcompeting native flowers one year but not the next. Suggest some factors that may have changed the competitive outcome.*

In a broader sense, however, the significance of interspecific competition rests not on a limited number of high profile effects, but on an answer to the question 'How widespread are the ecological and evolutionary consequences of interspecific competition in practice?' We address this question in two ways. In the first, dealt with in Section 6.5.1, we ask 'How prevalent is current competition in natural communities?'. To demonstrate current competition requires experimental field manipulations, in which one species is removed from or added to the community and the responses of the other species are monitored. It is important to answer this question, because where current competition is demonstrable, neither the ghost of competition past nor spatial and temporal variation are likely to have a crucial role. And, if current competition is prevalent, then interspecific competition is likely to be an important structuring force in nature. However, even if current competition is *not* prevalent, past competition, and therefore competition generally, may still have played a significant role in structuring communities.

The second problem, dealt with in Section 6.5.2, is to distinguish between interspecific competition (past or present) and 'mere chance': species differ not as a reflection of interspecific competition but because they *are* different species. The many studies in which experimental field manipulations have not been possible can be examined to determine whether observed patterns provide strong evidence for a role for competition, or are open to alternative interpretations.

### 6.5.1 The prevalence of current competition

There have been two classic surveys of field experiments on interspecific competition. Schoener (1983) examined the results of all the experiments he could

find – 164 studies in all. He found that approximately equal numbers of studies had dealt with terrestrial plants, terrestrial animals and marine organisms, but that studies of freshwater organisms amounted to only about half the number in the other groups. Amongst the terrestrial studies, however, he found that most were concerned with temperate regions and mainland populations, and that there were relatively few dealing with phytophagous (plant-eating) insects. Any conclusions were therefore bound to be subject to the limitations imposed by what ecologists had chosen to look at. Nevertheless, Schoener found that approximately 90% of the studies had demonstrated the existence of interspecific competition, and that the figures were 89%, 91% and 94% for terrestrial, freshwater and marine organisms, respectively. Moreover, even if he looked at single species or small groups of species (of which there were 390) rather than at whole studies, which may have dealt with several groups of species, he found that 76% showed effects of competition at least sometimes, and 57% showed effects in all the conditions under which they were examined. Once again, terrestrial, freshwater and marine organisms gave very similar figures.

surveys of published studies of competition indicate that current competition is widespread . . .

Connell's (1983) review was less extensive than Schoener's: 72 studies, dealing with a total of 215 species and 527 different experiments. Interspecific competition was demonstrated in most of the studies, more than half of the species and approximately 40% of the experiments. In contrast to Schoener, Connell found that interspecific competition was more prevalent in marine than in terrestrial organisms, and also that it was more prevalent in large than in small organisms.

Taken together, Schoener's and Connell's reviews certainly seem to indicate that active, current interspecific competition is widespread. Its percentage occurrence amongst species is admittedly lower than its percentage occurrence amongst whole studies, but this is to be expected, since, for example, if four species were arranged along a single niche dimension and all adjacent species competed with each other, this would still be only three out of six (or 50%) of all possible pairwise interactions.

. . . but these surveys exaggerate to an unknown extent the true frequency of competition

Connell also found, however, that in studies of just one pair of species, interspecific competition was almost always apparent, whereas with more species the prevalence dropped markedly (from more than 90% to less than 50%). This can be explained to some extent by the argument outlined above, but it may also indicate biases in the particular pairs of species studied, and in the studies that are actually reported (or accepted by journal editors). It is highly likely that many pairs of species are chosen for study because they are 'interesting' (because competition between them is suspected) and if none is found this is simply not reported. Judging the prevalence of competition from such studies is rather like judging the prevalence of debauched clergymen from the 'gutter press'. This is a real problem, only partially alleviated in studies on larger groups of species when a number of 'negatives' can be conscientiously reported alongside one or a few 'positives'. Thus the results of surveys, such as those by Schoener and Connell, exaggerate, to an unknown extent, the frequency of competition.

As previously noted, phytophagous insects were poorly represented in Schoener's data, but reviews of this group alone have tended to suggest either that competition is relatively rare in this group overall (Strong et al., 1984) or rare in at least certain types of phytophagous insects, for example 'leaf-biters' (Denno et al., 1995). On a more general level, it has been suggested that herbivores as a whole are seldom food-limited, and are therefore not likely to compete for common resources

(Hairston et al., 1960; Slobodkin et al., 1967). The bases for this suggestion are the observations that green plants are normally abundant and largely intact, they are rarely devastated, and most herbivores are scarce most of the time. Schoener found the proportion of herbivores exhibiting interspecific competition to be significantly lower than the proportions of plants, carnivores or detritivores.

Taken overall, therefore, current interspecific competition has been reported in studies on a wide range of organisms and in some groups its incidence may be particularly obvious, for example amongst sessile organisms in crowded situations. However, in other groups of organisms, interspecific competition may have little or no influence. It appears to be relatively rare among herbivores generally, and particularly rare amongst some types of phytophagous insect.

### 6.5.2 Competition or mere chance?

There is a tendency to interpret differences between the niches of coexisting species as confirming the importance of interspecific competition. But the theory of interspecific competition does more than predict 'differences'. It predicts not simply that the niches of competing species differ, but that they differ more than would be expected from chance alone. A more rigorous investigation of the role of interspecific competition, therefore, should address itself to the question: 'Does the observed pattern, even if it appears to implicate competition, differ significantly from the sort of pattern that could arise in the community even in the absence of any interactions between species?' This question has been the driving force behind analyses that seek to compare real communities with so-called *neutral models*. These are hypothetical models of actual communities that retain certain of the characteristics of their real counterparts, but reassemble or reconstruct some of the community components in a way that specifically excludes the consequences of interspecific competition. In fact, the neutral model analyses are attempts to follow a much more general approach to scientific investigation, namely the construction and testing of *null hypotheses*. The idea is that the data are rearranged into a form (the neutral model or null hypothesis) representing what the data would look like in the absence of interspecific competition. Then, if the actual data show a significant statistical difference from the null hypothesis, the null hypothesis is rejected and the action of interspecific competition is strongly inferred.

In fact, the approach has been applied to three different predictions of what a community structured by interspecific competition should look like: (i) potential competitors that coexist in a community should exhibit niche differentiation; (ii) this niche differentiation will often manifest itself as morphological differentiation; and (iii) within a community, potential competitors with little or no niche differentiation should not coexist, so each should tend to occur only where the other is absent ('negatively associated distributions'). The application of null hypotheses to community structure – that is, the reconstruction of natural communities with interspecific competition removed – has not been achieved to the satisfaction of all ecologists. But a brief examination of a study of niche differentiation in lizard communities shows the potential and rationale of the neutral model approach (Box 6.3). For these lizard communities, niches are more spaced out than would be expected by chance alone and interspecific competition therefore appears to play an important role in community structure.

neutral models

niche differentiation,  
morphological differentiation  
and negatively associated  
distributions



## 6.3 QUANTITATIVE ASPECTS

### 6.3 Quantitative aspects

#### Neutral models of lizard communities

Lawlor (1980) investigated differential resource utilization in 10 North American lizard communities, consisting of four to nine species. For each community, there were estimates of the amounts of each of 20 food categories consumed by each species. This pattern of resource use allowed the calculation, for each pair of species in a community, of an index

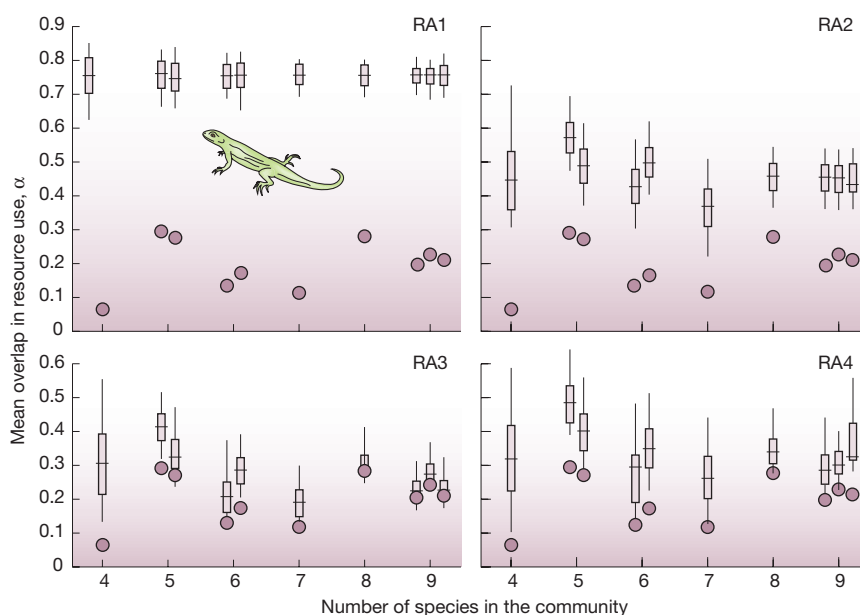
of *resource use overlap*, which varied between 0 (no overlap) and 1 (complete overlap). Each community was then characterized by a single value: the mean resource overlap for all pairs of species present.

A number of 'neutral models' of these communities were then created. They were of four types. The first type, for example, retained the minimum amount of original community structure. Only the original number of species and the original number of resource categories were retained. Beyond that, species were allocated food preferences completely at random, such that there were far fewer species completely ignoring food in particular categories than in the real community. The niche breadth of each species was therefore increased. The fourth type, on the other hand, retained most of the original community structure: if a species ignored food in a particular category, then that was left unaffected, but among those categories where food was eaten, preferences were reassigned at random. These neutral models were then compared with their real counterparts in terms of their patterns of resource use overlap. If competition is a significant force in determining community structure, then the niches should be spaced out, and resource use overlap in the real communities should be less – and statistically significantly less – than that in the neutral models.

The results (Figure 6.19) were that in all communities, and for all four neutral models, the model mean overlap was higher than that observed for the real community, and that in almost all cases this was statistically significant. For these lizard communities, therefore, the observed low overlaps in resource use suggest that niches are more segregated than would be expected by chance alone, and that interspecific competition plays an important role in community structure.



A desert lizard of the southwestern United States.



**Figure 6.19**

The mean indices of resource use overlap for each of 10 North American lizard communities are shown as solid circles. These can be compared, in each case, with the mean (horizontal line), standard deviation (vertical rectangle), and range (vertical line) of mean overlap values for the corresponding set of 100 randomly constructed communities. The analysis was performed using four different types of reorganization algorithms (RA1 to RA4).

AFTER LAWLOR, 1980

Where niche differentiation is manifested as morphological differentiation, the spacing out of niches can be expected to have its counterpart in regularity in the degree of morphological difference between species belonging to a guild. One example is shown in Figure 6.20 for four species of fossil strophomenide brachiopod (so-called ‘lamp shells’ that resemble bivalve mollusks) that appear from the fossil record to have coexisted. If successively sized species are compared, they have a consistent ratio for body outline length of around 1.5. Moreover, when Hermoyian et al. (2002) built 100,000 null models that each drew four species at random from the complete strophomenide brachiopod fossil fauna (74 taxa) and calculated size ratios between adjacent species, they rejected the null hypothesis that the observed ratios could have arisen from randomly selected taxa ( $P < 0.03$ ), supporting the hypothesis that competition had played a key role in structuring this community.

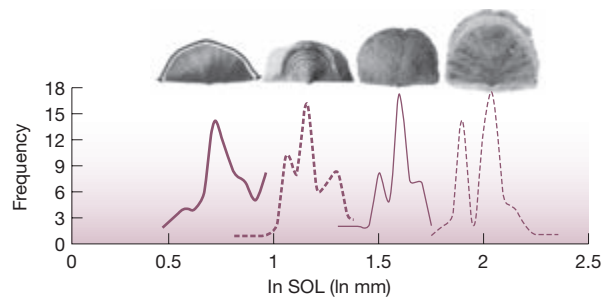
The null model approach to the analysis of distributional differences involves comparing the pattern of species co-occurrences at a suite of locations with what would be expected by chance. An excess of negative associations would then be consistent with a role for competition in determining community structure. Gotelli

morphological patterns

negatively associated distributions

**Figure 6.20**

Distributions of strophomenide body outline length (SOL) of samples of four coexisting species of brachiopods collected from a late Ordovician (ca. 448–438 million years before present) marine sediment in Indiana, USA. The species shown, from left to right, are *Eoconetes clarksvillensis*, *Leptaena richmondensis*, *Strophomena planumbona* and *Rafinesquina alternata*.



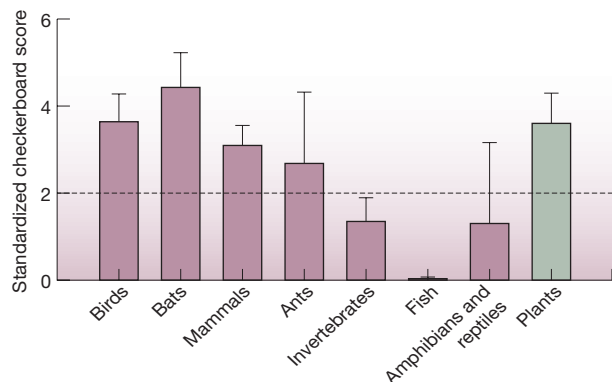
AFTER HERMOYAN ET AL., 2002

and McCabe (2002) carried out a ‘meta-analysis’: an analysis of all the analyses of others that they could find (96 data sets in all) that had examined the distribution of species assemblages across sets of replicated sites. For every real data set, a ‘checkerboard score’,  $C$ , was computed. This is highest when every species-pair in a community forms a perfect checkerboard: sites are either ‘black’ or ‘white’ – the species never co-occur. It takes its lowest value when all species-pairs always co-occur. Next, 1000 randomized versions of each data set were simulated and  $C$  calculated each time. The observed  $C$ -value for each data set was then expressed as the number of standard deviations it was,  $C_s$ , from the mean of the simulations. The null hypothesis is that  $C_s$  should be zero (real communities not different from simulated communities), but in particular that a  $C_s$ -value greater than 2 indicates a significant negative association between species in the data set. The results, classified by taxonomic group, are shown in Figure 6.21. There was a significant excess of negative associations for plants and homeothermic vertebrates and for ants, but the excess was not significant for invertebrates (other than ants), fish, amphibians and reptiles.

This kind of pattern – sometimes a role for competition is confirmed, sometimes not – has been the general conclusion from the neutral model approach. What then should be our verdict on it? Perhaps most fundamentally, its aim is undoubtedly worthy. It concentrates the minds of investigators, stopping them from jumping to conclusions too readily; it is important to guard against the temptation to see competition in a community simply because we are looking for it. On the other hand, the approach can never take the place of a detailed understanding of the field ecology of the species in question, or of manipulative experiments designed to reveal competition by increasing or reducing species abundances. It, like so many other approaches, can only be part of the community ecologist’s armory.

**Figure 6.21**

An analysis of data sets of species distributions across sites, classified by taxonomic group (mean  $\pm$  SE) seeking evidence of an excess of negative associations, as measured by the standardized ‘checkerboard score’ (see text). The dashed line indicates an effects size of 2.0, which is the approximate 5% significance level.



AFTER GOTELLI &amp; MCCABE, 2002





## Summary

### SUMMARY

#### Ecological effects of interspecific competition

The essence of interspecific competition is that individuals of one species suffer a reduction in fecundity, survivorship or growth as a result of exploitation of resources or interference by individuals of another species.

Species are often excluded by interspecific competition from locations at which they could exist perfectly well in the absence of interspecific competition.

With exploitation competition, the more successful competitor is the one that more effectively exploits shared resources. Two species exploiting two resources can compete but still coexist when each species holds one of the resources at a level that is too low for effective exploitation by the other species.

A fundamental niche is the combination of conditions and resources that allow a species to exist when considered in isolation from any other species. Whereas its realized niche is the combination of conditions and resources that allow it to exist in the presence of other species that might be harmful to its existence – especially interspecific competitors.

The Competitive Exclusion Principle states that if two competing species coexist in a stable environment, then they do so as a result of differentiation of their realized niches. If, however, there is no such differentiation, or if it is precluded by the habitat, then one competing species will eliminate or exclude the other. However, whenever we see coexisting species with different niches it is not reasonable to jump to the conclusion that this is the principle in operation.

The only true test for whether competition occurs between species is to manipulate the abundance of each competitor and observe the response of its counterparts.

Environments are usually a patchwork of favorable and unfavorable habitats; patches are often only available temporarily; and patches often appear at unpredictable times and in unpredictable places.

Under such variable conditions, competition may only rarely 'run its course'.

#### Evolutionary effects of interspecific competition

Although species may not be competing now, their ancestors may have competed in the past. We can expect species to have evolved characteristics that ensure that they compete less, or not at all, with members of other species. Coexisting present-day competitors, and coexisting species that have evolved an avoidance of competition, can look, at least superficially, the same.

By invoking something that cannot be observed directly – 'the ghost of competition past' – it is impossible to prove an evolutionary effect of interspecific competition. However, careful observational studies have sometimes revealed patterns that are difficult to explain in any other way.

#### Interspecific competition and community structure

Interspecific competition tends to structure communities by acting within guilds – groups of species exploiting the same class of resource in a similar fashion.

Niche complementarity can be discerned in some communities, where coexisting species that occupy a similar position along one niche dimension tend to differ along another dimension.

Niches can be differentiated through differential resource utilization. In many cases, however, differential resource utilization expresses itself as either a microhabitat differentiation between the species or a difference in geographic distribution. Alternatively, differential resource utilization may express itself as a temporal separation between species. Niches can also be differentiated on the basis of conditions. This too can express itself as either a microhabitat differentiation, or a difference in geographic distribution, or a temporal separation.

### How significant is interspecific competition in practice?

Surveys of published studies of competition indicate that current competition is widespread but these exaggerate to an unknown extent the true frequency of competition.

The theory of interspecific competition predicts that the niches of competing species should be arranged regularly rather than randomly in niche space, that as

a reflection of this they should be more distinct morphologically than expected by chance, and that competitors should be negatively associated in their distributions. Neutral models have been developed to determine what the community pattern would look like in the absence of interspecific competition. Real communities are sometimes structured in a way that makes an influence of competition difficult to deny.

## Review questions

### REVIEW QUESTIONS

Asterisks indicate challenge questions

- 1 Some experiments concerning interspecific competition have monitored both the population densities of the species involved and their impact on resources. Why is it helpful to do both?
- 2 Interspecific competition may be a result of exploitation of resources or of direct interference. Give an example of each and compare their consequences for the species involved.
- 3 Define fundamental niche and realized niche. How do these concepts help us to understand the effects of competitors?
- 4 With the help of one plant and one animal example, explain how two species may coexist by holding different resources at levels that are too low for effective exploitation by the other species.
- 5\* Define the Competitive Exclusion Principle. When we see coexisting species with different niches is it reasonable to conclude that this is the principle in action?
- 6 Explain how environmental heterogeneity may permit an apparently 'weak' competitor to coexist with a species that might be expected to exclude it.
- 7\* What is the 'ghost of competition past'? Why is it impossible to prove an evolutionary effect of interspecific competition?
- 8 Provide one example each of niche differentiation involving physiological, morphological and behavioral properties of coexisting species. How may these differences have arisen?
- 9 Define 'niche complementarity' and, with the help of an example, explain how it may help to account for the coexistence of many species in a community.
- 10\* Discuss the pros and cons of the neutral model approach to evaluating the effects of competition on community composition.

# Chapter 7



## Predation, grazing and disease

### *Chapter contents*

#### CHAPTER CONTENTS

- 7.1 Introduction
- 7.2 Prey fitness and abundance
- 7.3 The subtleties of predation
- 7.4 Predator behavior: foraging and transmission
- 7.5 Population dynamics of predation
- 7.6 Predation and community structure

### *Key concepts*

#### KEY CONCEPTS

In this chapter you will:

- distinguish the similarities and differences among ‘true predators’, grazers and parasites
- understand the subtleties of predation, including the capacity of prey to compensate
- appreciate the value of the optimal foraging approach for analyzing predator choices
- recognize the underlying tendency of populations of predators and prey to cycle and the ‘damping’ effect of crowding and patchy distributions
- understand the consequences of predation for community composition

*Every living organism is either a consumer of other living organisms, or is consumed by other living organisms, or – in the case of most animals – is both. We cannot hope to understand the structure and dynamics of ecological populations and communities until we understand the links between consumers and their prey.*

## 7.1 Introduction

predator: a term extending beyond the obvious examples

Ask most people to name a predator and they are almost certain to say something like lion, tiger or grizzly bear – something big, ferocious, instantly lethal. However, from an ecological point of view, a predator may be defined as any organism that consumes all or part of another living organism (its prey or host) thereby benefiting itself, but reducing the growth, fecundity or survival of the prey. Thus, this definition extends beyond the likes of lions and tigers by including organisms that consume all *or part* of their prey and also those that merely *reduce* their prey's growth, fecundity or survival. Predators are not all large, aggressive or instantly lethal – they need not even be animals. Here we examine these consumers together and try to understand the part they play in determining the structure and dynamics of ecological systems.

Within the broad definition, three main types of predator can be distinguished.

'true' predators, grazers and parasites

### 1 'True' predators:

- invariably kill their prey and do so more or less immediately after attacking them;
- consume several or many prey items in the course of their life.

True predators therefore include lions, tigers and grizzly bears, but also spiders, baleen whales that filter plankton from the sea, zooplanktonic animals that consume phytoplankton, birds that eat seeds (each one an individual organism) and carnivorous plants.

### 2 Grazers:

- attack several or many prey items in the course of their life;
- consume only part of each prey item;
- do not usually kill their prey, especially in the short term.

Grazers therefore include cattle, sheep and locusts, but also, for example, blood-sucking leeches that take a small, relatively insignificant blood meal from several vertebrate prey over the course of their life.

### 3 Parasites:

- consume only part of each prey item (usually called their host);
- do not usually kill their prey, especially in the short term;
- attack one or very few prey items in the course of their life, with which they therefore often form a relatively intimate association.

Parasites therefore include some obvious examples: animal parasites and pathogens such as tapeworms and the tuberculosis bacterium, plant pathogens like tobacco mosaic virus, parasitic plants like mistletoes, and the tiny wasps that form ‘galls’ on oak leaves. But aphids that extract sap from one or a very few plants with which they enter into an intimate association, and even caterpillars that spend their whole life on one host plant, are also, in effect, parasites.

On the other hand, these distinctions between ‘true’ predators, grazers and parasites, as with most categorizations of the living world, have been drawn in large part for convenience – certainly not because every organism fits neatly into one and only one category. We could, for example, have included a fourth class, the *parasitoids*, which are little known to non-biologists but are extensively studied by ecologists (and immensely important in the biological control of insect pests; see Chapter 12). Parasitoids are flies and wasps whose larvae consume their insect larva host from within, having been laid there as an egg by their mother. Parasitoids therefore straddle the ‘parasite’ and ‘true predator’ categories (only one host individual, which it always kills), fitting neatly into neither and confirming the impossibility of constructing clear boundaries.

There is, moreover, no satisfactory term to describe all the ‘animal consumers of living organisms’ to be discussed in this chapter. Detritivores and plants are also ‘consumers’ (of dead organisms, or of water, radiation, and so on); whilst the term ‘predator’ inevitably tends to suggest a ‘true’ predator even after we have defined it to encompass grazers and parasites too. But neither is it very satisfactory to be continually using the qualifier ‘true’ when discussing conventional predators. Thus, throughout this chapter, ‘predator’ will often be used as a shorthand term to encompass true predators, grazers and parasites, when general points are being made; but it will also be used to refer to predators in the more conventional sense, when it is obvious that this is what is being done.

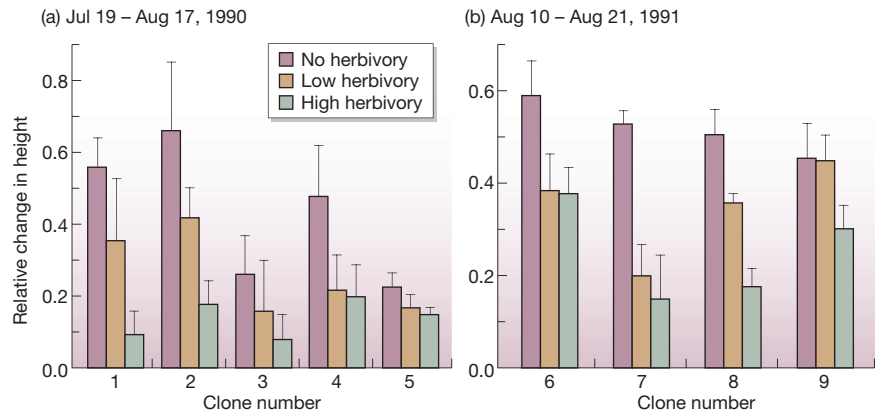
parasitoids – and the artificiality of boundaries



A parasitoid wasp, which uses its long ovipositor to insert its eggs into the larvae of other insects, where they develop by consuming their host.

**Figure 7.1**

Relative growth rates (changes in height, with standard errors) of a number of different clones of the sand-dune willow, *Salix cordata*, in 1990 (a) and in 1991 (b), subjected either to no herbivory, low herbivory (four flea beetles per plant) or high herbivory (eight beetles per plant).



AFTER BACH, 1994

## 7.2 Prey fitness and abundance

predators reduce the fecundity and/or survival of individual prey

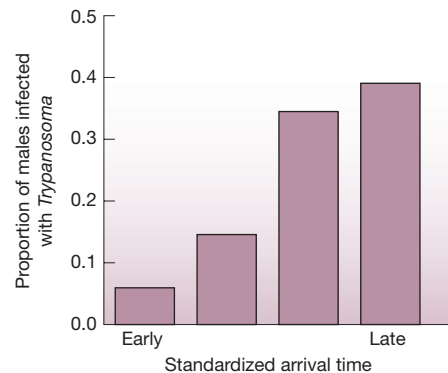
The fundamental similarity between predators, grazers and parasites is that each, in obtaining the resources it needs, reduces either the fecundity or the chances of survival of individual prey and may therefore reduce prey abundance. The effects of true predators on the survival of individual prey hardly need illustrating – the prey die. But the effects of grazers and parasites can be equally profound, if more subtle, as illustrated by the following two examples.

When the sand-dune willow, *Salix cordata*, was grazed by a flea beetle in two separate years – 1990 and 1991 – the reduction in the growth rate of the willow was marked in both years (Figure 7.1), but the consequences were rather different. Only in 1991 were the plants also subject to a severe shortage of water. Thus it was only in 1991 that the reduced growth rate was translated into plant mortality: 80% of the plants died in the high grazing treatment, 40% died in the low grazing treatment, but none of the ungrazed control plants died.

The pied flycatcher is a bird that migrates early each summer from tropical West Africa to Finland (and elsewhere in northern Europe) to breed. Males that arrive relatively early are particularly successful at finding mates. Late arrival therefore has a serious detrimental effect on the expected ‘fecundity’ of a male: the number of offspring that it can expect to father. Significantly, the later arrivals are disproportionately infected with the blood parasite *Trypanosoma* (Figure 7.2).

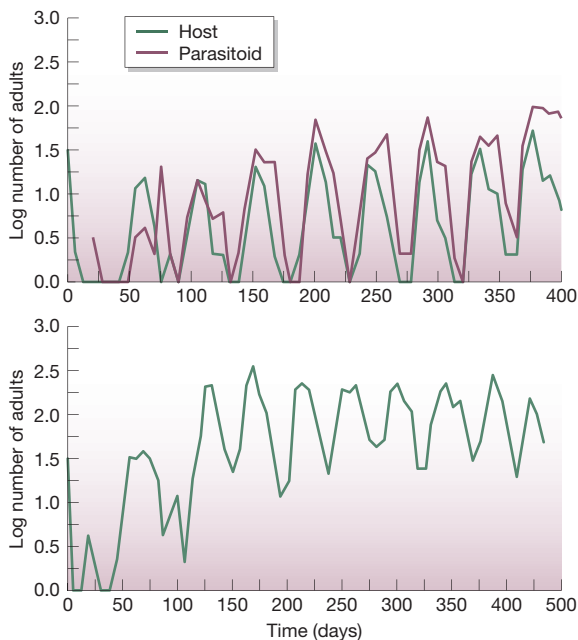
**Figure 7.2**

The proportion of males of male pied flycatchers (*Ficedula hypoleuca*) infected with *Trypanosoma* amongst groups of migrants arriving in Finland at different times.



AFTER RÄTTI ET AL., 1993



**Figure 7.3**

Long-term population dynamics in laboratory population cages of a host (*Plodia interpunctella*), with and without its parasitoid (*Venturia canescens*). (a) Host and parasitoid, and (b) the host alone.

Infection with the parasite therefore has a profound effect on the reproductive output of individual birds.

It is not so straightforward, though, to demonstrate that reductions in the survival or fecundity of individual prey translate into reductions in prey abundance – we need to be able to compare prey populations in the presence and the absence of predators. As so often in ecology, we cannot rely simply on observation: we need experiments – either ones we set up ourselves, or natural experiments set up for us by nature.

For example, Figure 7.3 contrasts the dynamics of laboratory populations of an important pest, the Indian meal moth, with and without a parasitoid wasp, *Venturia canescens*. Ignoring the rather obvious regular fluctuations (cycles) in both moth and wasp, it is apparent that the wasp reduced moth abundance to less than one-tenth of what it would otherwise be (notice the logarithmic scale in the figure).

A particularly graphic example of the impact grazers can have is provided by the story of the invasion of Lake Moon Darra in North Queensland (Australia) by *Salvinia molesta*, a water fern that originated in Brazil. In 1978, the lake carried an infestation of 50,000 metric tons of the fern. In *Salvinia*'s native habitat in Brazil, the black long-snouted weevil (*Cyrtobagous* spp.) was known to graze only on *Salvinia*. Hence in June 1980, 1500 adults were released at an inlet to the lake and a further release was made in January 1981. By April 1981, *Salvinia* was dying throughout the lake, supporting an estimated population of one billion beetles. By August 1981, less than 1 metric ton of *Salvinia* remained. This was a 'controlled' experiment in that other lakes in the region continued to bear large populations of *Salvinia*.

All sorts of predators can cause reductions in the abundance of their prey. We shall see as this chapter develops, however, that they do not *necessarily* do so.

predators *can* reduce prey abundance – but do not *necessarily* do so

## 7.3 The subtleties of predation

There is much to be gained by stressing the similarities between different types of predators. On the other hand, it would be wrong to make this an excuse for oversimplification (there *are* important differences between true predators, grazers and parasites), or to give the impression that all acts of predation are simply a question of ‘prey dies, predator takes one step closer to the production of its next offspring’.

### 7.3.1 Interactions with other factors

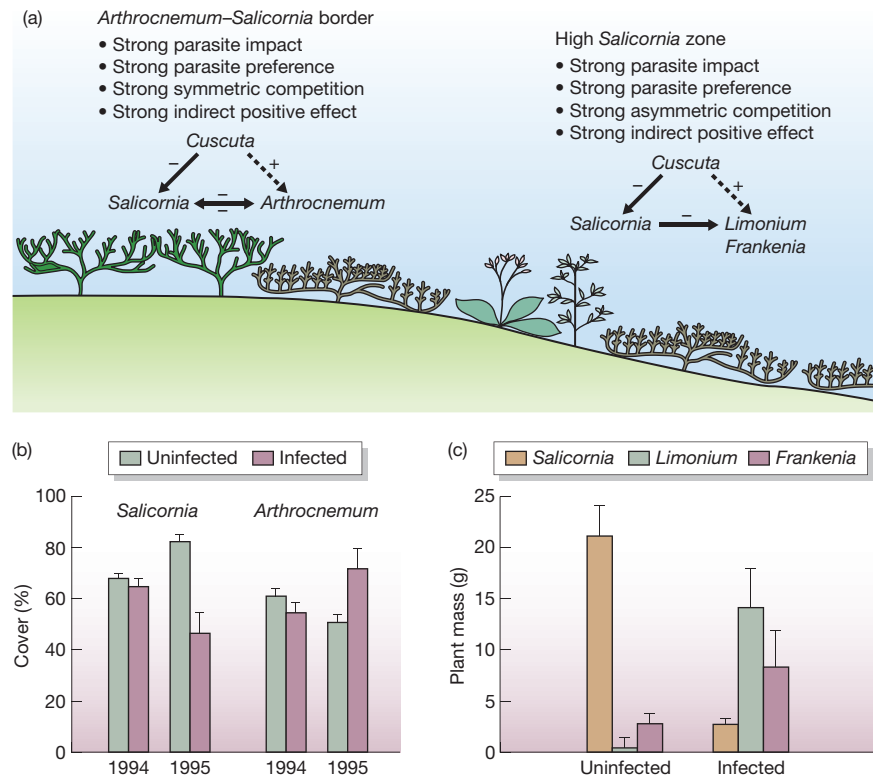
grazers and parasites may make prey more vulnerable to other forms of mortality

Grazers and parasites, in particular, often exert their harm not by killing their prey immediately like true predators, but by making the prey more vulnerable to some other form of mortality. For example, grazers and parasites may have a more drastic effect than is initially apparent because of an interaction with competition between the prey. This can be seen in a southern Californian salt marsh, where the parasitic plant, dodder (*Cuscuta salina*) attacks a number of plants including *Salicornia* (Figure 7.4). *Salicornia* tends to be the strongest competitor in the marsh, but it is also the preferred host of dodder. The distribution of plants in the marsh can therefore only be understood as a result of the interaction between competition and parasitism (Figure 7.4).

Infection or grazing may also make hosts or prey more susceptible to predation. For example, postmortem examination of red grouse (*Lagopus lagopus scoticus*) showed that birds killed by predators in the spring and summer carried significantly

**Figure 7.4**

The effect of dodder, *Cuscuta salina*, on competition between *Salicornia* and other species in a southern Californian salt marsh. (a) A schematic representation of the main plants in the community in the upper and middle zones of the marsh and the interactions between them (solid arrows: direct effects; dashed arrows: indirect effects). *Salicornia* (the relatively low growing plant in the figure) is most attacked by, dodder (which is not itself shown in the figure); but when uninfected, *Salicornia* competes strongly and symmetrically with *Arthrocnemum* at the *Arthrocnemum*–*Salicornia* border, and is a dominant competitor over *Limonium* and *Frankenia* in the middle (high *Salicornia*) zone. However, dodder significantly shifts the competitive balances. (b) Over time, *Salicornia* decreased and *Arthrocnemum* increased in plots infected with dodder. (c) Large patches of dodder suppress *Salicornia* and favor *Limonium* and *Frankenia*.



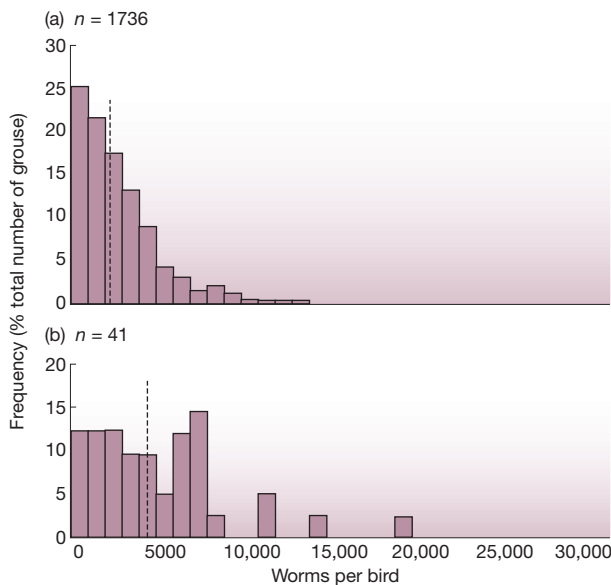


Figure 7.5

Infection with a nematode worm parasite makes red grouse more susceptible to predation. (a) Worm burdens of birds that are shot for 'sport', which may be taken as a representative sample of the whole population. (b) Worm burdens of those found killed by predators. The vertical line is the mean in each case, and the worm burdens of those caught by predators are clearly higher, typically, than those in the population as a whole.

AFTER HUDSON ET AL., 1992

greater burdens of the gut nematode parasite *Trichostrongylus tenuis* than the birds that remained in the fall (Figure 7.5).

### 7.3.2 Compensation and defense by individual prey

The effects of parasites and grazers, however, are not always more profound than they first seem. They are often *less* profound because, for example, individual plants can compensate in a variety of ways for the effects of herbivory (Strauss & Agrawal, 1999). The removal of leaves from a plant may decrease the shading of other leaves and thereby increase their rate of photosynthesis. Or, following herbivore attack, many plants compensate by utilizing stored reserves. Herbivory frequently alters the distribution of newly synthesized material within the plant, usually maintaining a balanced root : shoot ratio. When shoots are defoliated, an increased fraction of net production is channeled to the shoots themselves; when roots are destroyed, the switch is towards the roots. Often, there is compensatory regrowth of defoliated plants when buds that would otherwise remain dormant are stimulated to develop. There is also commonly a reduced subsequent death rate of surviving plant parts.

For example, when herbivory on the biennial plant field gentian (*Gentianella campestris*) was simulated by clipping to remove half its biomass (Figure 7.6a), subsequent production of fruits was increased (Figure 7.6b), but the outcome depended on the timing of clipping. Fruit production was much increased over controls if clipping occurred between July 12 and 20, but if clipping occurred later than this, fruit production was less in clipped plants than in unclipped controls. The period when the plants show compensation coincides with the time when damage by herbivores normally occurs.

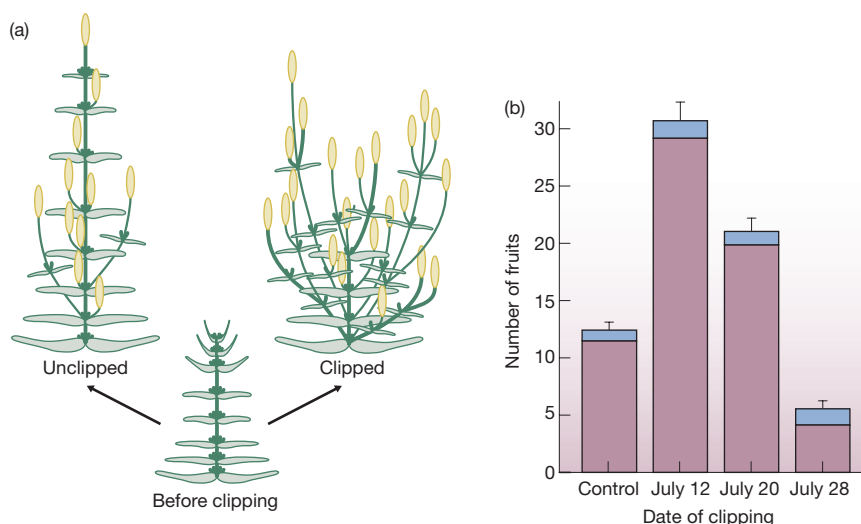
Plants may also respond by initiating or increasing their production of defensive structures or chemicals. For example, a few weeks of grazing on the brown seaweed *Ascophyllum nodosum* by snails (*Littorina obtusata*) induced substantially increased

compensatory plant responses

defensive plant responses

**Figure 7.6**

(a) Clipping of field gentians to simulate herbivory causes changes in the architecture and numbers of flowers produced. (b) Production of mature (maroon histograms) and immature fruits (blue histograms) of unclipped control plants and plants clipped on different occasions from July 12 to 28, 1992. Means and standard errors are shown and all means are significantly different from each other ( $P < 0.05$ ). Plants clipped on July 12 and 20 developed significantly more fruits than unclipped controls. Plants clipped on July 28 developed significantly fewer fruits than controls.



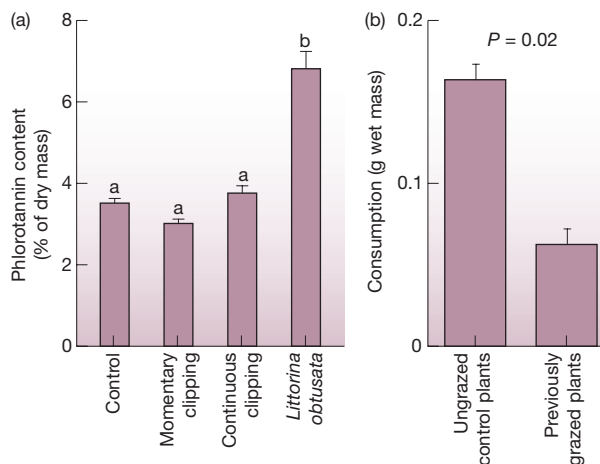
AFTER LENNARTSSON ET AL., 1998

concentrations of phlorotannins (Figure 7.7a), which reduce further snail grazing (Figure 7.7b). Interestingly, simple clipping of the plants did not have the same effect. The snails can stay and feed on the same plant for long time periods. Induced responses that take time to develop can still be effective in reducing damage.

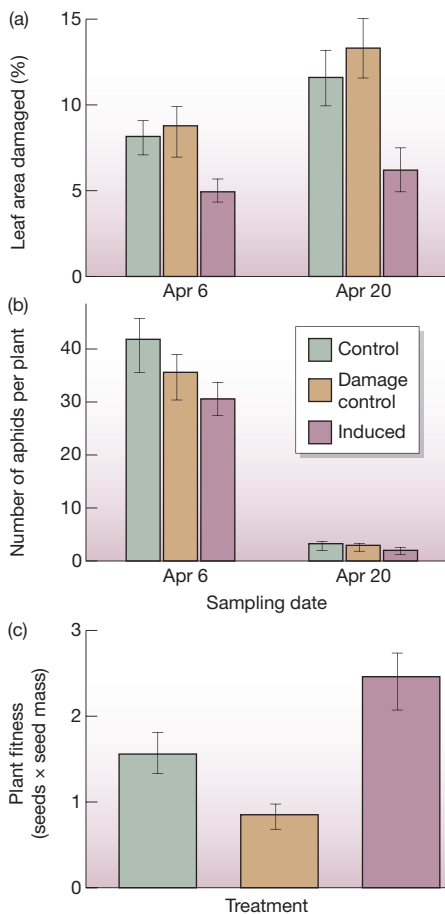
The snails in Figure 7.7 suffer as a consequence of the seaweed's response (they eat less), and the plants benefit in that less of them is eaten. But that benefit comes to the plants at a cost (that of producing the chemicals), and it is therefore never straightforward to establish whether plants experience a net benefit in the longer term. One attempt to address this question looked at lifetime fitness of wild radish plants (*Raphanus sativus*) assigned to one of three treatments: (i) grazed by caterpillars, *Pieris rapae*; (ii) leaf-damage controls (an equivalent amount of biomass removed using scissors); and (iii) overall controls (undamaged). Earwigs (*Forficula* spp.) and other chewing herbivores caused 100% more leaf damage on control and damage control plants than on grazed plants, and there were 30% more phloem-sucking aphids on them (Figure 7.8a, b): the response induced

**Figure 7.7**

(a) Phlorotannin content of *Ascophyllum nodosum* plants after exposure to simulated herbivory (removing tissue with a hole punch) or grazing by the snail *Littorina obtusata*. Only the snail had the effect of inducing increased concentrations of the defensive chemical in the seaweed. Means and standard errors are shown. Different letters indicate that means are significantly different ( $P < 0.05$ ). (b) In a subsequent experiment, the snails were presented with algal shoots from the control and the snail-grazed treatments in (a) – the snails ate significantly less of plants with high phlorotannin content.



AFTER PAVIA &amp; TOTH 2000

**Figure 7.8**

(a) Percentage leaf area consumed by chewing herbivores and (b) number of aphids per plant, measured on two dates (April 6 and 20) in three field treatments: overall control, damage control (tissue removed by scissors) and induced (caused by grazing of caterpillars of *Pieris rapae*). (c) Fitness of plants in the three treatments calculated by multiplying the number of seeds produced by the mean seed mass (in milligrams).

AFTER AGRAWAL, 1998

by the caterpillars protected the plants from additional herbivory. Moreover, despite any costs, this increased significantly (by more than 60%) the lifetime fitness of induced plants compared to the control plants. Plants cut with scissors, on the other hand, had 38% *lower* fitness than the overall controls, emphasizing the negative effect of tissue loss without the benefits of induction (Figure 7.8c). This fitness benefit occurred, however, only in environments containing herbivores. In their absence, the costs of producing the chemicals outweighed the benefits and plants suffered a reduction in fitness (Karban et al., 1999). Thus the benefits in the presence of herbivores were *net* benefits: benefits outweighed costs.

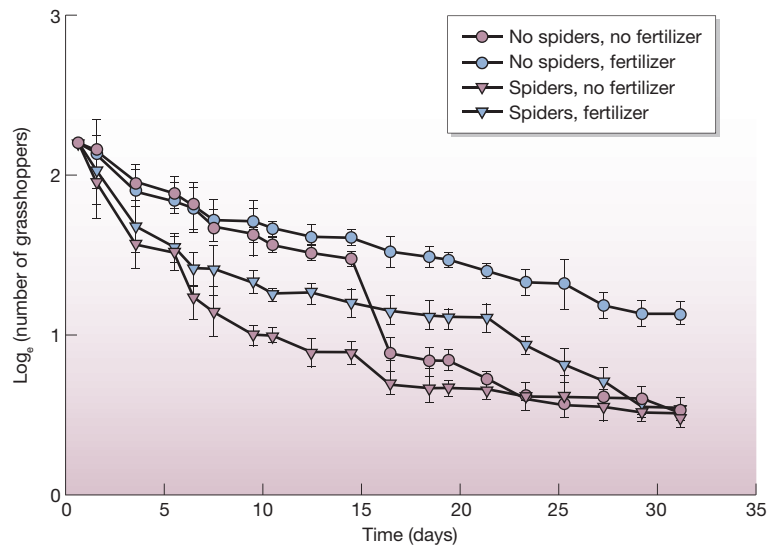
### 7.3.3 From individual prey to prey populations

In spite of these various qualifications, the general rule is that predators are harmful to individual prey. But the effects of predation on a population of prey are not always so predictable. The impact of predation is most commonly limited by compensatory reactions amongst the survivors as a result of reduced intraspecific competition. Outcomes of predation may, therefore, vary with food availability. When there is plenty of good food, and no competition, the effects of predation should be detectable. But when food is short and competition intense, predation

compensatory reactions amongst  
surviving prey . . .

**Figure 7.9**

Trajectories of numbers of grasshoppers surviving (mean  $\pm$  SE) for fertilizer and predation treatment combinations in a field experiment involving caged plots in the Arapaho Prairie, Nebraska, USA.



AFTER OEDERIKOVEN & JOERN, 2000

may relieve competitive pressures and allow individuals to survive who would not otherwise do so. The results of an experiment that tested this are shown in Figure 7.9. The survival of grasshoppers (*Ageneotettix deorum*) was monitored in caged prairie plots with food (grass) that was either plentiful (fertilized) or limited (not fertilized), and in the presence or absence of predatory spiders. As predicted, with plentiful food, spider predation reduced the numbers surviving: a non-compensatory response. But with limited food, spider predation and food limitation were compensatory: the same numbers of grasshoppers were recovered at the end of the 31-day experiment.

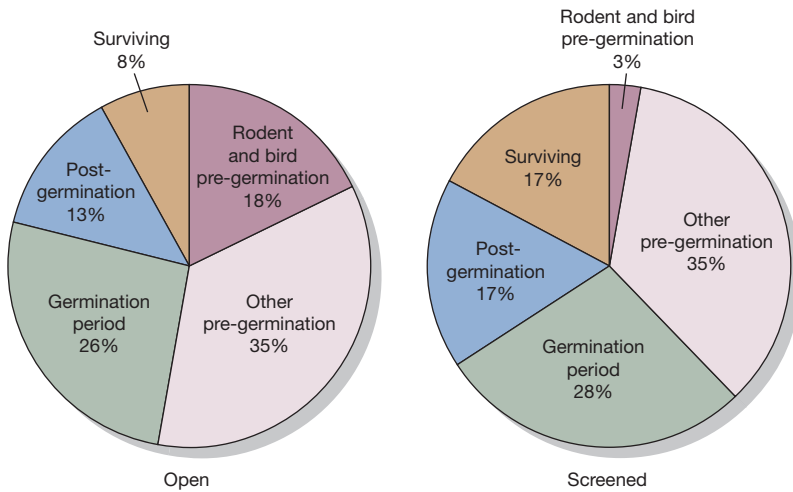
Predation may also have a negligible impact on prey abundance if an increased loss of prey to predators at one stage of the prey's life simply leads to a decreased loss to predators at some other stage. If, for example, recruitment to a population of adult plants is not limited by the number of seeds produced, then insects that reduce seed production are unlikely to have an important effect on plant population dynamics. The point is illustrated by a study of the shrub, *Haplopappus venetus*, in California (Louda, 1982, 1983). The level of insect damage to the developing flowers and seeds was high. Experimental exclusion of flower and seed predators, therefore, caused a 104% increase in the number of developing seeds escaping damage. This led to an increase in the number of seedlings established. But subsequently this was followed by a much greater loss of seedlings, probably to vertebrate herbivores. As a consequence, original abundances were re-established in spite of the short-term importance of the seed predators.

... but compensation is often imperfect

Compensation, however, is by no means always perfect. Figure 7.10, for example, shows the results of an experiment in which Douglas fir seeds were sown both in open plots and in plots screened from rodents and birds. The immediate effect of this was an enormous reduction in the loss of seeds (though the screens were not totally effective). There were, however, compensatory *increases* in mortality from other causes. Nonetheless, in spite of this, the overall effect of screening was to more than double the number of seedlings still surviving 1 year after germination.



AFTER LAWRENCE &amp; REDISKE, 1962

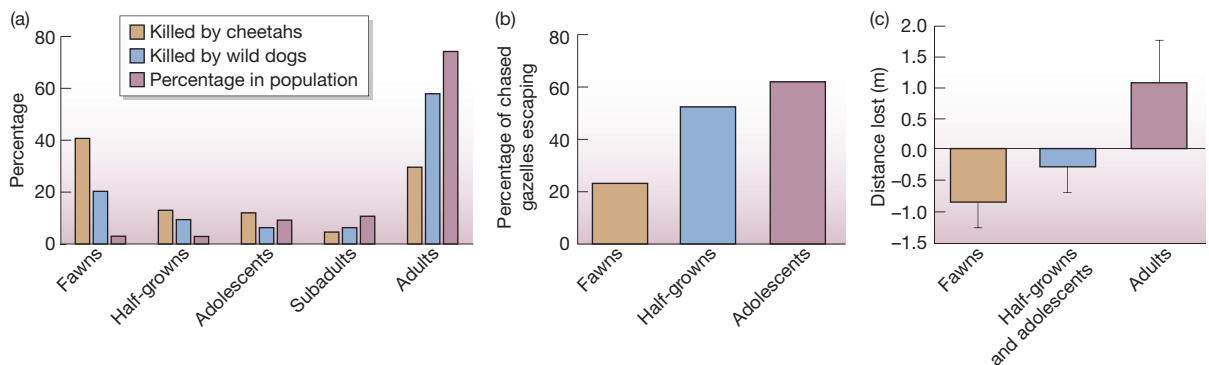
**Figure 7.10**

When Douglas fir seeds are protected from vertebrate predation by screens, the lowered mortality is compensated for (but not *fully* compensated for) by increased mortality from other sources.

Predators may also have little impact on prey populations as a whole because of the particular individuals they attack. Many large carnivores, for example, concentrate their attacks on the old (and infirm), on the young (and naive) or on the sick. Thus, a study in the Serengeti found that cheetahs and wild dogs killed a disproportionate number from the younger age classes of Thomson's gazelles (Figure 7.11a) because: (i) these young animals were easier to catch (Figure 7.11b); (ii) they had lower stamina and running speeds; (iii) they were less good at outmaneuvering the predators (Figure 7.11c); and (iv) they may even have failed to recognize the predators. The effects of predation on the prey population will therefore have been less than would otherwise have been the case, because these young gazelles will have been making no present reproductive contribution to the population, and many would have died anyway, from other causes, before they were able to do so.

predators often attack the weakest and most vulnerable

AFTER FITZGIBBON &amp; FANSHAW, 1989; FITZGIBBON, 1990

**Figure 7.11**

(a) The proportions of different age classes (determined by tooth wear) of Thomson's gazelles in cheetah and wild dog kills is quite different from their proportions in the population as a whole. (b) Age influences the probability for Thomson's gazelles of escaping when chased by cheetahs. (c) When prey (Thomson's gazelles) zigzag to escape chasing cheetahs, prey age influences the mean distance lost by the cheetahs.

Thomson's gazelle.



It is apparent, then, that the effects of a predator on an individual prey are crucially dependent on the response of the prey; and the effects on prey populations are equally dependent on which prey are attacked and on the responses of other prey individuals and other natural enemies of the prey. The effect of a predator may be more drastic than it appears, or less drastic. It is only rarely what it seems.

## 7.4 Predator behavior: foraging and transmission

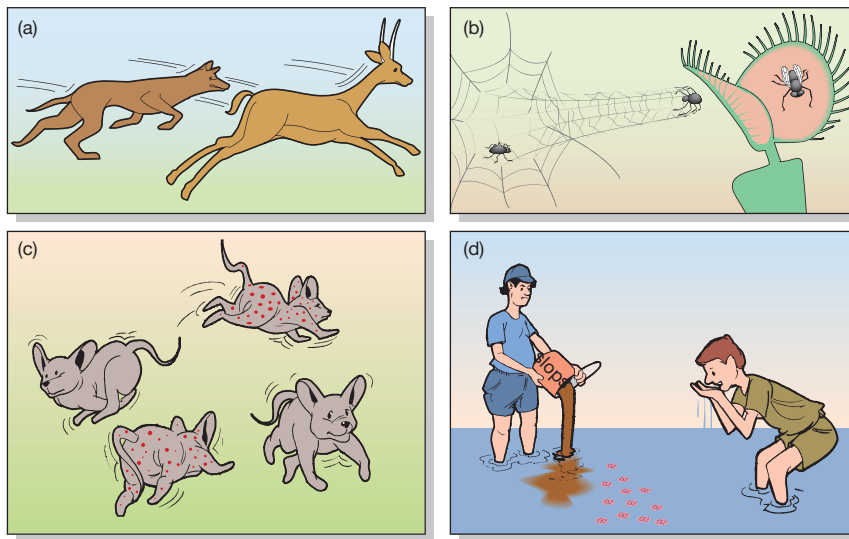
So far, we have been looking, in effect, at what happens *after* a predator finds its prey. Now, we take a step back and examine how contact is established in the first place. This is crucially important, because this pattern of contact is critical in determining the predator's consumption rate, which goes a long way to determining its own level of benefit and the harm it does to the prey, which determines, in turn, the impact on the dynamics of predator and prey populations, and so on.

sit-and-wait predators

True predators and grazers typically 'forage'. Many move around within their habitat in search of their prey, and their pattern of contact is therefore itself determined by the predators' behavior – and sometimes by the evasive behavior of the prey (Figure 7.12a). This foraging behavior is discussed below. Other predators, web-spinning spiders for instance, 'sit and wait' for their prey, though almost always in a location they have selected (Figure 7.12b).

parasite transmission

With parasites and pathogens, on the other hand, we usually talk about transmission rather than foraging. This may be direct transmission between infectious and uninfected hosts when they come into contact with one another (Figure 7.12c), or free-living stages of the parasite may be released from infected hosts, so that it is the pattern of contact between these and uninfected hosts that is important (Figure 7.12d). The simplest assumption we can make for directly transmitted parasites – and one that often is made when attempting to understand their dynamics (discussed in Section 7.5) – is that transmission depends on infectious and uninfected hosts 'bumping into one another'. In other words, the overall rate of parasite transmission depends both on the density of uninfected, susceptible hosts (since these represent the size of the 'target') and on the density of infectious hosts (since this represents the risk of the target being 'hit') (Figure 7.12c).

**Figure 7.12**

The different types of foraging and transmission. (a) Active predators seeking (possibly active) prey. (b) Sit-and-wait predators waiting for active prey to come to them. (c) Direct parasite transmission – infectious and uninfected hosts ‘bumping into each other’. (d) Transmission between free-living stages of a parasite shed by a host and new, uninfected hosts.

### 7.4.1 Foraging behavior

There are many questions we might ask about the behavior of a foraging predator. Where, within the habitat available to it, does it concentrate its foraging? How long does it tend to remain in one location before moving on to another? And so on. Ecologists address all such questions from two points of view. The first is from the viewpoint of the *consequences* of the behavior for the dynamics of predator and prey populations. We turn to this in Section 7.5.

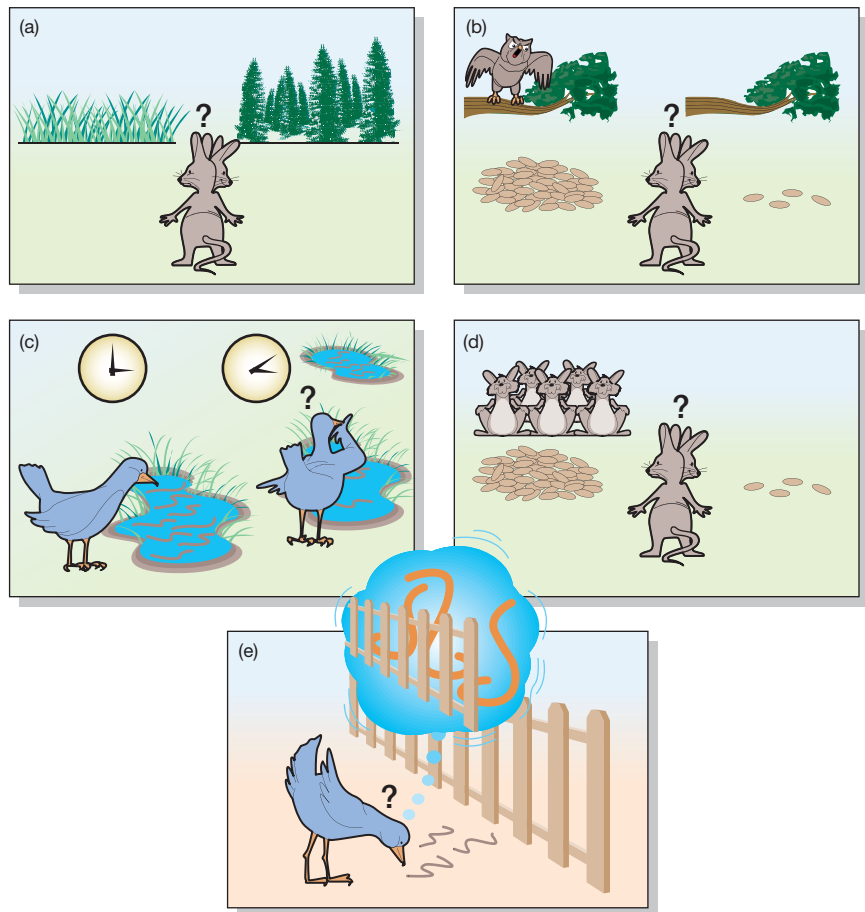
The second is the viewpoint of ‘behavioral ecology’ or ‘optimal foraging’. The aim is to seek to understand why particular patterns of foraging behavior have been favored by natural selection. Most readers will be familiar with the general approach as applied, for example, to the anatomy of the bird’s wing – we may seek to understand why a particular surface area, or a particular arrangement of feathers, has been favored by natural selection for the effectiveness they bring to the bird’s powers of flight. Of course, this does not imply even a basic understanding of aerodynamics theory on the bird’s part – only that those birds with the most effective wings have been favored in the past by natural selection and have passed their effectiveness on to their offspring. Likewise, in applying this approach to foraging behavior, there is no question of suggesting ‘conscious decision-making’ on the predator’s part.

What, though, is the appropriate measure of ‘effectiveness’ in foraging behavior – the equivalent of flying ability as a criterion for a successful bird’s wing? Usually, the *net* rate of energy intake has been used – that is, the amount of energy obtained per unit time, *after* account has been taken of the energy expended by the predator in carrying out its foraging. For many consumers, however, the efficient gathering of energy may be less critical than some other dietary constituent (e.g. nitrogen), or it may be of prime importance for the forager to consume a mixed and balanced diet. The predictions of optimal foraging theory do not apply to all the foraging decisions of every predator.

the evolutionary, optimal foraging approach

**Figure 7.13**

The types of foraging 'decisions' considered by optimal foraging theory. (a) Choosing between habitats. (b) The conflict between increasing input and avoiding predation. (c) Patch stay-time decisions. (d) The 'ideal free' decision – the conflict between patch quality and competitor density. (e) Optimal diets – to include or not to include an item in the diet (when something better might be 'round the corner').



applying the optimal foraging approach to a range of foraging behaviors

A range of the aspects of foraging behavior to which the optimal foraging approach has been applied is illustrated in Figure 7.13. These are elaborated on briefly here, before the whole approach is demonstrated by examining just one of them in detail.

- Where, within the habitat available to it, does a predator concentrate its foraging (Figure 7.13a)? Does it concentrate where the long-term expectation of net energy intake is highest *or* where the risk of extended periods of low intake is lowest?
- Does the location chosen by a predator reflect just the expected energy intake? Or does there appear to be some balancing of this against the risk of being preyed upon by its own predators (Figure 7.13b)?
- How long does a predator tend to remain in one location – one patch, say, of a patchy environment – before moving on to another (Figure 7.11c)? Does it remain for extended periods and hence avoid unproductive trips from one patch to another? Or does it leave patches early, before the resources there are depleted?
- What are the effects of other, competing predators foraging in the same habitat (Figure 7.11d)? The expected net energy intake from a location is

now presumably a reflection of both its intrinsic productivity and the number of competing foragers. What is the expected distribution of the predators as a whole over the various habitat patches?

- The remaining ‘question’, in Figure 7.13e, and the one to which we now turn in Box 7.1 for a fuller illustration of the optimal foraging approach, is that of *diet width*. No predator can possibly be capable of consuming all types of prey. Simple design constraints prevent shrews from eating owls (even though shrews are carnivores) and prevent humming-birds from eating seeds. Even within their constraints, however, most animals consume a narrower range of food types than they are morphologically capable of consuming.



## 7.1 Quantitative aspects

### 7.1 QUANTITATIVE ASPECTS

#### Optimal diet width

Diet width is the range of food types consumed by a predator. In order to derive widely applicable predictions about when diets are likely to be broad or narrow, we need to strip down the act of foraging to its bare essentials. So, we can say that to obtain food, any predator must expend time and energy, first in searching for its prey, and then in handling it (i.e. pursuing, subduing and consuming it). While searching, a predator is likely to encounter a wide variety of food items. Diet width, therefore, depends on the responses of predators once they have encountered prey. Generalists, those with a broad diet, pursue a large proportion of the prey they encounter. Specialists, those with a narrow diet, continue searching except when they encounter prey of their specifically preferred type.

Generalists have the advantage of spending relatively little time searching – most of the items they find they pursue and, if successful, consume. But they suffer the disadvantage of including relative low-profitability items in their diet. That is, generalists enjoy a net intake of energy much of the time – but their *rate* of intake is often relatively low. Specialists, on the other hand, have the advantage of only including high-profitability items in their diet. But they suffer the disadvantage of spending a relatively large amount of their time searching for them. Thus, specialists spend

relatively long periods with a net expenditure of energy – but when they do take in energy it is at a relatively high rate. Determining the predicted optimal foraging strategy for a particular predator amounts to determining how these pros and cons should be balanced so as to maximize the *overall* net rate of energy intake, while searching for *and* handling prey (MacArthur & Pianka, 1966; Charnov, 1976).

We can start by taking it for granted that any predator will include the single most profitable type of prey in its diet: that is, the one for which the net rate of energy intake is highest. But should it include the next most profitable type of item too? Or, when it comes across such an item, should it ignore it and carry on searching for the *most* profitable type? And if it does include the second most profitable type, what about the third, and the fourth? And so on.

Consider first this ‘second most profitable food type’. When will it pay a predator to include an item of this type in its diet (in energetic terms)? The answer is when, having found the item, its expected rate of energy intake over the time spent handling it exceeds its expected rate of intake if, instead, it continued to search for, and then handled, an item of the *most* profitable type. (The *expected* times are simply the average times for items of a particular type.) Expressing this in symbols, we call the expected searching

and handling times for the most profitable type  $s_1$  and  $h_1$ , and its energy content  $E_1$ , and the expected handling time for the second most profitable type  $h_2$ , and its energy content  $E_2$ . Then it pays the predator to increase the width of its diet if  $E_2/h_2$  (i.e. the rate of intake, energy per unit time, if it handles the second-best type) is greater than  $E_1/(s_1 + h_1)$  (the rate of intake if instead it searches for the most profitable type).

Suppose now that it did pay the predator to expand its diet. What about the third most profitable type? We argue in the same way as before: it will pay a predator to include this in its diet if, when it has

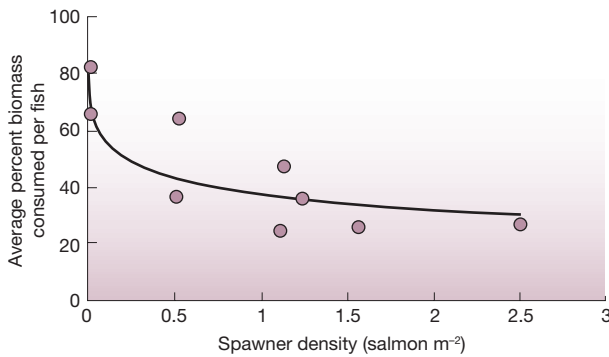
found it, its expected rate of intake over the time spent handling it,  $h_3$ , exceeds the expected rate if it searches for and handles *either* of the two most profitable types, both already included in its diet. Thus, if we call  $\bar{s}$ ,  $\bar{h}$ , and  $\bar{E}$  the searching and handling times and energy content for items already in the diet, it will pay the predator to expand its diet if  $E_3/h_3$  exceeds  $\bar{E}/(\bar{s} + \bar{h})$ , or, more generally, if  $E_n/h_n$  exceeds  $\bar{E}/(\bar{s} + \bar{h})$ , where  $n$  refers generally to the 'next' most profitable prey type (not already in the diet). The ecological implications of this rule are considered in the main text.

#### predictions of the optimal diet model

In summary, Box 7.1 suggests that a predator should continue to add increasingly less profitable items to its diet as long as this increases its overall rate of energy intake. This will serve to maximize its overall rate of energy intake. This 'optimal diet model', then, leads to a number of predictions.

- 1 Predators with handling times that are typically short compared to their search times should be generalists (i.e. have broad diets), because in the short time it takes them to handle a prey item that has already been found, they can barely begin to search for another prey item. This prediction seems to be supported by the broad diets of many insectivorous birds feeding in trees and shrubs. Searching is always moderately time-consuming, but handling the minute, stationary insects takes negligible time and is almost always successful. A bird, therefore, has something to gain and virtually nothing to lose by consuming an item once found, and overall profitability is maximized by a broad diet.
- 2 By contrast, predators with handling times that are long relative to their search times should be specialists: maximizing the rate of energy intake is achieved by including only the most profitable items in the diet. For instance, lions live more or less constantly in sight of their prey so that search time is negligible; handling time, on the other hand, and particularly pursuit time, can be long (and very energy-consuming). Lions consequently specialize on those prey that can be pursued most profitably: the immature, the lame and the old.
- 3 Other things being equal, a predator should have a broader diet in an unproductive environment (where prey items are relatively rare and search times relatively large) than in a productive environment (where search times are generally smaller). This prediction is supported by a study of brown and black bears (*Ursos arctos* and *U. americanus*) feeding on salmon in Bristol Bay in Alaska (Figure 7.14). When salmon availability was high, bears consumed less biomass per captured fish, targeting energy-rich fish (those that had not spawned) or energy-rich body parts (eggs in females, brain in males). That is, their diet became more specialized when prey were abundant.



**Figure 7.14**

As the spawning density (i.e. the abundance) of salmon increases, the average percentage of each salmon consumed by bears decreases: as prey abundance increases, the predators become more specialized.

Overall, then, we can see how an evolutionary, optimal foraging approach can help us make sense of predators' foraging behavior – how it makes predictions of what that behavior might be expected to be, and that these predictions may be supported by real examples.

## 7.5 Population dynamics of predation

What roles do predators play in driving the dynamics of their prey, or prey play in driving the dynamics of their predators? Are there common patterns of dynamics that emerge? The preceding sections should have made it plain that there are no simple answers to these questions. It depends on the detail of the behavior of individual predators and prey, on possible compensatory responses at individual and population levels, and so on. Rather than despair at the complexity of it all, however, we can build an understanding of these dynamics by starting simply and then adding additional features one by one to construct a more realistic picture.

building a picture from simple beginnings

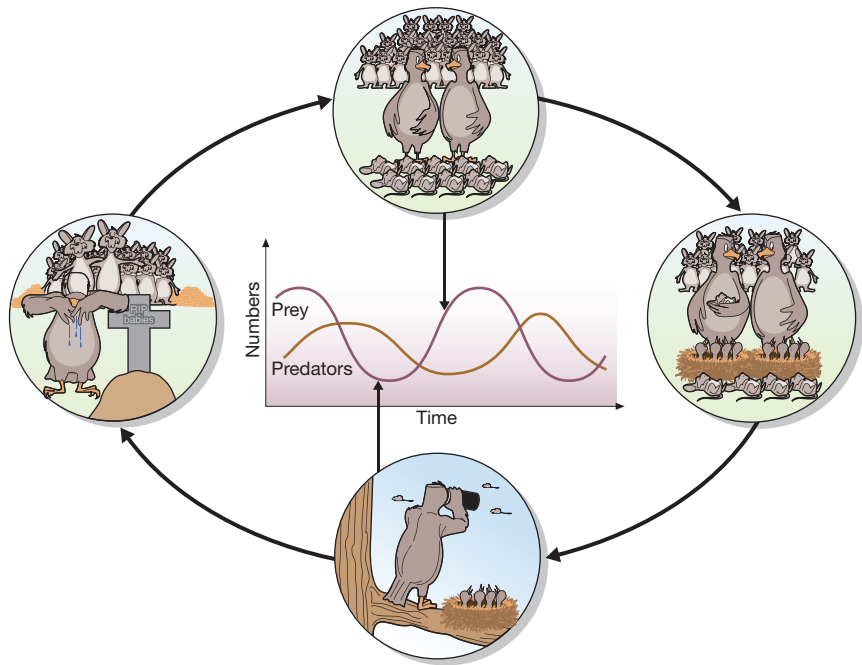
### 7.5.1 Underlying dynamics of predator–prey interactions: a tendency to cycle

We begin by consciously oversimplifying – ignoring everything but the predator and the prey, and asking what underlying tendency there might be in the dynamics of their interaction. It turns out that the underlying tendency is to exhibit coupled oscillations – cycles – in abundance. With this established, we can turn to the many other important factors that might modify or override this underlying tendency. Rather than explore each and every one of them, however, Sections 7.5.4 and 7.5.5 examine just two of the more important ones: crowding and spatial patchiness. These two factors cannot, of course, tell the whole story; but they illustrate how the differences in predator–prey dynamics, from example to example, might be explained by the varying influences of the different factors with a potential impact on those dynamics.

Starting simply then, suppose there is a large population of prey. Predators presented with this population should do well: they should consume many prey and hence increase in abundance themselves. The large population of prey thus gives rise to a large population of predators (Figure 7.15). But this increasing

**Figure 7.15**

The underlying tendency for predators and prey to display coupled oscillations in abundance as a result of the time delays in their responses to each other's abundance.



population of predators increasingly takes its toll of the prey. The large population of predators therefore gives rise to a small population of prey. Now the predators are in trouble: large numbers of them and very little food. Their abundance declines. But this takes the pressure off the prey: the small population of predators gives rise to a large population of prey – and the populations are back to where they started. There is, in short, an underlying tendency for predators and their prey to undergo coupled oscillations in abundance – population cycles (Figure 7.15) – essentially because of the time delays in the response of predator abundance to that of the prey, and vice versa. (A ‘time delay’ in response means, for example, that a high predator abundance reflects a high prey abundance *in the past*, but it *coincides* with declining prey abundance, and so on.) A simple mathematical model – the Lotka–Volterra model – conveying essentially the same message is described in Box 7.2.

### 7.5.2 Predator–prey cycles in practice

the ‘expectation’ of cycles is only rarely fulfilled

This underlying tendency for predator–prey interactions to generate coupled oscillations in abundance could produce an ‘expectation’ of such cycles in real populations, but there were many aspects of predator and prey ecology that had to be ignored in order to demonstrate this underlying tendency, and these can greatly modify expectations. It is no surprise, then, that there are rather few good examples of clear predator–prey cycles – albeit ones that have received a great deal of attention from ecologists. Nonetheless, in trying to make sense of predator–prey population dynamics, cycles – the underlying tendency – are a good place to start.



## 7.2 Quantitative aspects

### 7.2 QUANTITATIVE ASPECTS

#### The Lotka–Volterra predator–prey model

Here, as in Boxes 5.4 and 6.1, one of the foundation-stone mathematical models of ecology is described and explained. The model is known (like the model of interspecific competition in Box 6.1) by the name of its originators: Lotka and Volterra (Volterra, 1926; Lotka, 1932). It has two components:  $P$ , the numbers present in a predator (or consumer) population, and  $N$ , the numbers or biomass present in a prey or plant population.

It is assumed that in the absence of consumers the prey population increases exponentially (see Box 5.4):

$$dN/dt = rN$$

But now we also need a term signifying that prey individuals are removed from the population by predators. They will do this at a rate that depends on the frequency of predator–prey encounters, which will increase with increasing numbers of predators ( $P$ ) and prey ( $N$ ). The exact number encountered and consumed, however, will also increase with the searching and attacking efficiency of the predator, denoted by  $a$ . The consumption rate of prey will thus be  $aPN$ , and overall:

$$dN/dt = rN - aPN \quad (1)$$

Turning to predator numbers, in the absence of food these are assumed to decline exponentially through starvation:

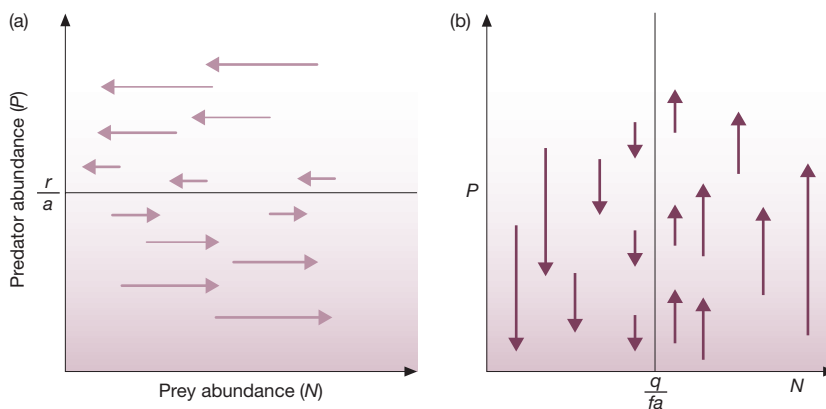
$$dP/dt = -qP$$

where  $q$  is their mortality rate. But this is counteracted by predator birth, the rate of which is assumed to depend on: (i) the rate at which food is consumed,  $aPN$ ; and (ii) the predator's efficiency,  $f$ , at turning this food into predator offspring. Overall:

$$dP/dt = faPN - qP \quad (2)$$

Equations 1 and 2 constitute the Lotka–Volterra model.

The properties of this model can be investigated by finding zero isoclines (see Box 6.1). There are separate predator and prey zero isoclines, both of which are drawn on a graph of prey density (x-axis) against predator density (y-axis) (Figure 7.16). The prey zero isocline joins combinations of predator and prey densities that lead to an unchanging prey population,  $dN/dt = 0$ , while the predator zero isocline joins



**Figure 7.16**

See box text for details.

combinations of predator and prey densities that lead to an unchanging predator population,  $dP/dt = 0$ .

In the case of the prey, we 'solve' for  $dN/dt = 0$  in equation 1, giving the equation of the isocline as:

$$P = r/a$$

Thus, since  $r$  and  $a$  are constants, the prey zero isocline is a line for which  $P$  itself is a constant (Figure 7.16a): prey increase when predator abundance is low ( $P < r/a$ ) but decrease when it is high ( $P > r/a$ ).

Similarly, for the predators, we solve for  $dP/dt = 0$  in equation 2, giving the equation of the isocline as:

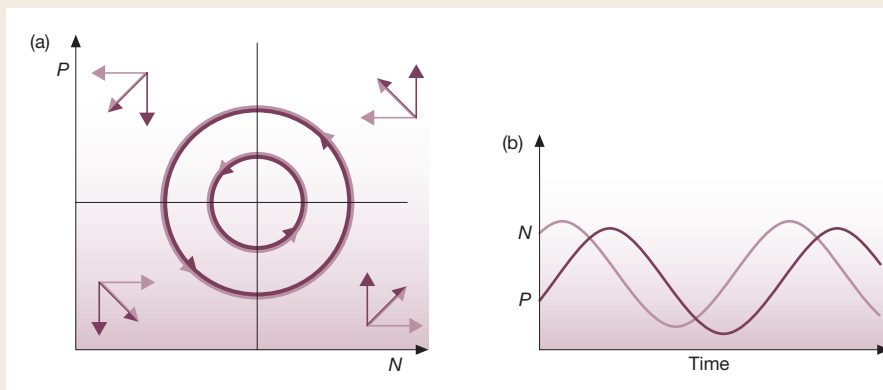
$$N = q/fa$$

The predator zero isocline is therefore a line along which  $N$  is constant (Figure 7.16b): predators decrease

when prey abundance is low ( $N < q/fa$ ) but increase when it is high ( $N > q/fa$ ).

Putting the two isoclines (and two sets of arrows) together in Figure 7.17 shows the behavior of joint populations. The various combinations of increases and decreases, listed above, mean that the populations undergo 'coupled oscillations' or 'coupled cycles' in abundance; 'coupled' in the sense that the rises and falls of the predators and prey are linked, with predator abundance tracking that of the prey (discussed biologically in the main text).

It is important to realize, however, that the model does not 'predict' the exact patterns of abundance that it generates. The world is much more complex than imagined by the model. But it does capture the essential tendency for coupled cycles in predator–prey interactions.

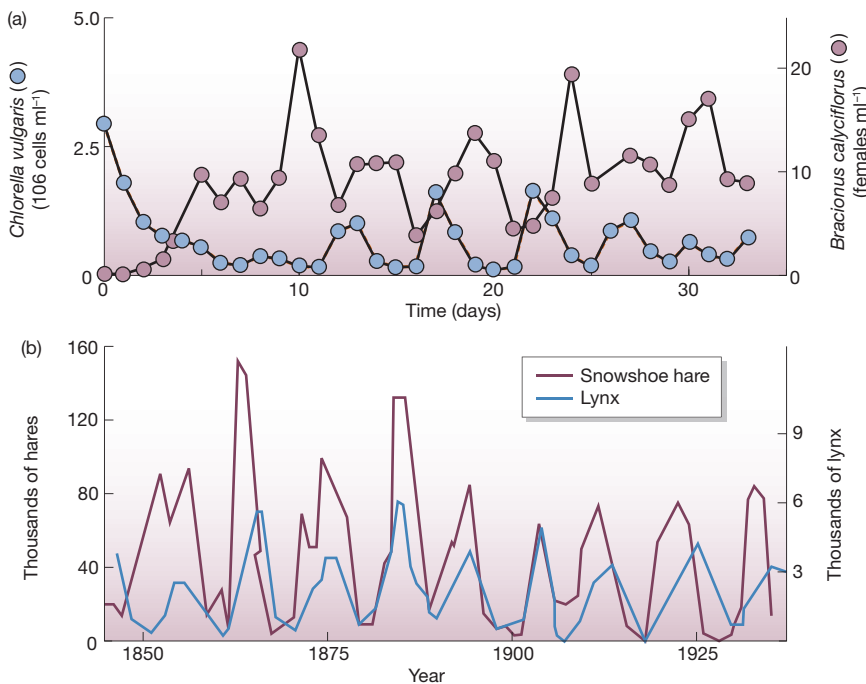


**Figure 7.17**

See box text for details.

plants, hares and lynx in  
North America . . .

They do occur sometimes. It has been possible in several cases, for example, to generate coupled predator–prey oscillations, several generations in length, in the laboratory (Figure 7.18a; see also Figure 7.22c). Amongst field populations, there are a number of examples in which regular cycles of prey and predator abundance can be discerned. Cycles in hare populations, in particular, have been discussed by ecologists since the 1920s, and were recognized by fur trappers more than 100 years earlier. Most famous of all is the snowshoe hare, *Lepus americanus*, which in the boreal forests of North America follows a '10-year cycle' (although in reality this varies in length between 8 and 11 years; see Figure 7.18b). The snowshoe hare is the dominant herbivore of the region, feeding on the terminal twigs of numerous shrubs and small trees. A number of predators, including the Canada lynx (*Lynx canadensis*), have associated cycles

**Figure 7.18**

Coupled oscillations in the abundance of predators and prey. (a) Parthenogenetic female rotifers, *Bracionus calyciflorus* (predators, maroon circles), and unicellular green algae, *Chlorella vulgaris* (prey, blue circles), in laboratory cultures. (b) The snowshoe hare (*Lepus americanus*) and the Canada lynx (*Lynx canadensis*) as determined by the number of pelts lodged with the Hudson Bay Company.

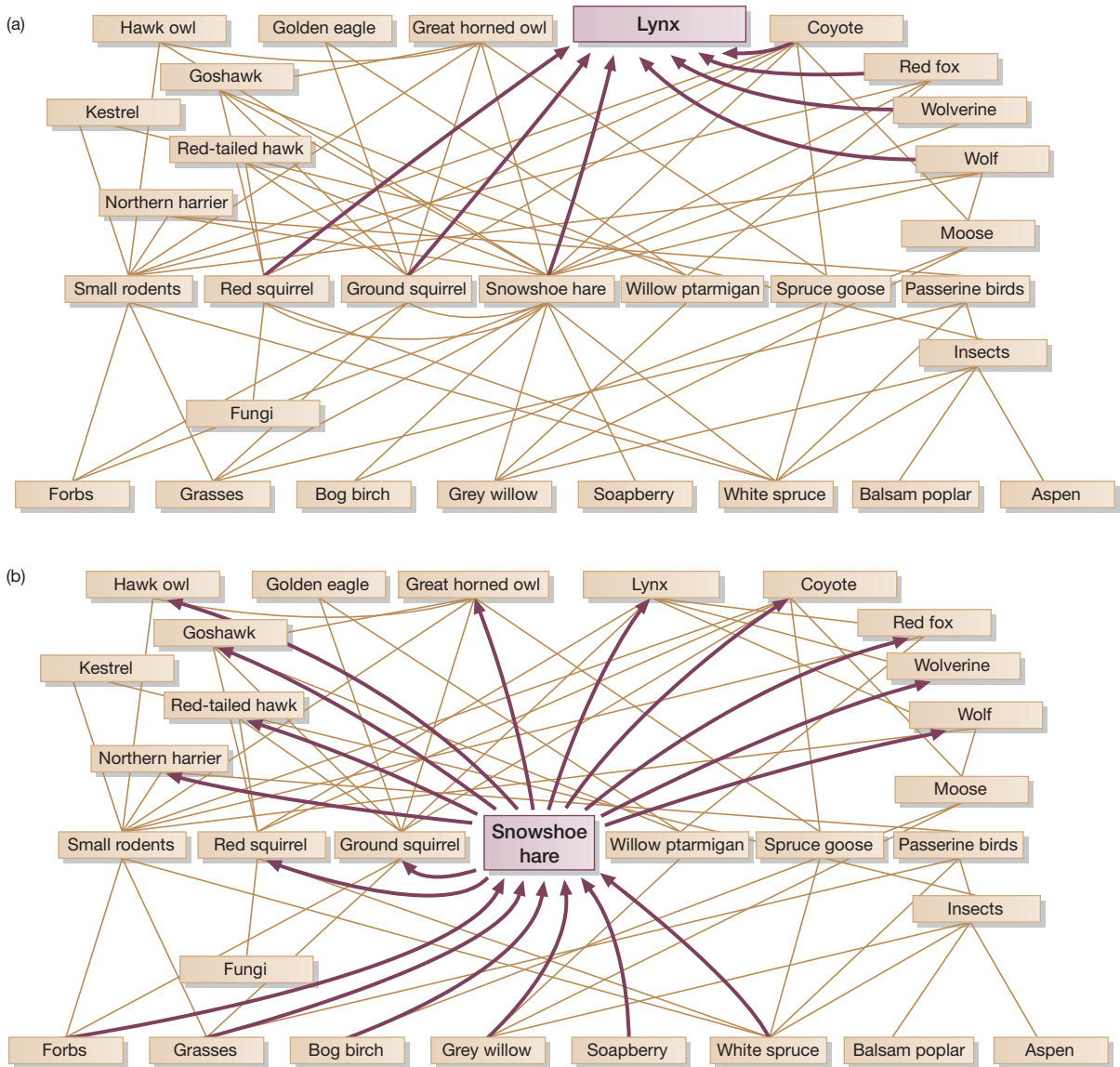


The Canada lynx and the snowshoe hare – a predator and prey that may show coupled oscillations.

of similar length. The hare cycles often involve 10–30-fold changes in abundance, and 100-fold changes can occur in some habitats. They are made all the more spectacular by being virtually synchronous over a vast area from Alaska to Newfoundland.

But are the hare and lynx participants in a predator–prey cycle? This immediately seems less likely once one appreciates the number of other species with which both interact. Their food web (see Section 9.5) is shown in Figure 7.19. In fact, both experimental studies (Krebs et al., 2001) and statistical analyses of the population dynamics data (Stenseth et al., 1997) suggest that whereas the dynamics of the hares are driven by their interactions with both their food and their predators (especially lynx), the dynamics of the lynx are driven largely by their interaction with their hare prey, much as the food web might suggest. Both the hare–plant and the predator–hare interactions have some propensity

... but how are the cycles generated?



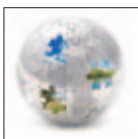
**Figure 7.19**

(a) The main species and groups of species in the boreal forest community of North America, with trophic interactions (who eats who) indicated by lines joining the species, and those affecting the Canada lynx shown as maroon arrows, pointing toward the consumer. (b) The same community, but with the interactions of the snowshoe hare shown as arrows.

to cycle on their own – but in practice the cycle seems normally to be generated by the interaction between the two. This warns us that even when we have a predator–prey pair both exhibiting cycles, we may still not be observing simple predator–prey oscillations.

Apparent instances of predator–prey cycles sometimes make the news – see Box 7.3 for an example.





## 7.3 Topical ECOncerns

### 7.3 TOPICAL ECOncerns

#### A cyclical outbreak of a forest insect in the news

Large outbreaks of forest tent caterpillars occur about every 10 years, and each lasts for 2–4 years. During these outbreaks, massive damage is done to the foliage of forest trees over large tracks of land. This article appeared in the *Telegraph Herald* (Dubuque, Iowa) on June 11, 2001.

##### Caterpillars making a meal out of northern forests

Forest tent caterpillars have munched their way through much of northern Wisconsin, eating aspen, sugar maple, birch and oak from Tomahawk to southern Canada.

The insects move across roads in waves that make the pavement seem to crawl and hang from trees in large clumps. . . . 'One lady from Eagle River said they were on her house and on her driveway and on her sidewalk, and she was ready to move back to Oak Creek', said Jim Bishop, public affairs manager for the Department of Natural Resource's northern region.

Shane Weber, a DNR forest entomologist from Spooner, said the caterpillars on sidewalks, driveways and highways are a good sign. 'Whenever they start these mass overland moves, suddenly moving in waves across the ground, it means that they're starving, looking for another source of food', he said.

In Superior, customers have inundated Dan's Feed Bin [general store], looking for ways to rid their yards and homes of the insects. Employee Amy Connor said some customers held their telephones up to the window so Connor could hear the worms falling like hail. 'It's terribly gross', she said.

The caterpillars have eaten most of the leaves in the Upper Peninsula, said Jeff Forslund, of Hartland, who drove to Ramsey, Michigan. 'My grandfather has about 500 acres of aspen, and there isn't a leaf left', Forslund said.

Most of the trees will survive and the caterpillars should start spinning cocoons by mid-June, the DNR said. Forest entomologist Dave Hall said he expects the outbreak to peak this year. 'I can't imagine it getting much worse', he said. The last infestation of the native forest tent caterpillars in Wisconsin was in the late 1980s and early 1990s. . . . During the last tent caterpillar outbreak, several serious traffic collisions in Canada were blamed on slick roads from squashed tent caterpillars.

About 4 million of the fuzzy crawlers can be found per acre at the peak of the cyclical infestation, the DNR said.

(All content © 2001 *Telegraph Herald* (Dubuque, IA) and may not be republished without permission.)

- 1 From what you have learnt about population cycles in this chapter, suggest an ecological scenario to account for the periodic outbreaks of these caterpillars.
- 2 Do you believe the comment attributed to a Department of Natural Resources (DNR) employee that the mass movement of the caterpillars is a good sign? How would you determine whether this behavior heralds an end to the peak phase of the cycle?

### 7.5.3 Disease dynamics and cycles

basic reproductive rate and the transmission threshold

Cycles are also apparent in the dynamics of many parasites, especially micro-parasites (bacteria, viruses, etc.). To understand the dynamics of any parasite, the best starting point is its basic reproductive rate, conventionally called 'R nought',  $R_0$ . For microparasites,  $R_0$  is the average number of new infected hosts that would arise from a single infectious host in a population of susceptible hosts. An infection will eventually die out for  $R_0 < 1$  (each present infection leads to less than one infection in the future), but an infection will spread for  $R_0 > 1$ . There is therefore a 'transmission threshold' when  $R_0 = 1$ , which must be crossed if a disease is to spread. A derivation of  $R_0$  for microparasites with direct transmission (see Figure 7.12c) is given in Box 7.4.

threshold population sizes and microparasite cycles

Box 7.4 provides us with a crucial insight into disease dynamics – for each directly transmitted microparasite there is a critical threshold population size that needs to be exceeded for a parasite population to be able to sustain itself. For example, measles has been calculated to have a threshold population size of around 300,000 individuals and is unlikely to have been of great importance until quite recently in human biology. However, it has generated major epidemics in the growing cities of the industrialized world in the 18th and 19th centuries, and in the growing concentrations of population in the developing world in the



## 7.4 Quantitative aspects

### Transmission threshold for microparasites

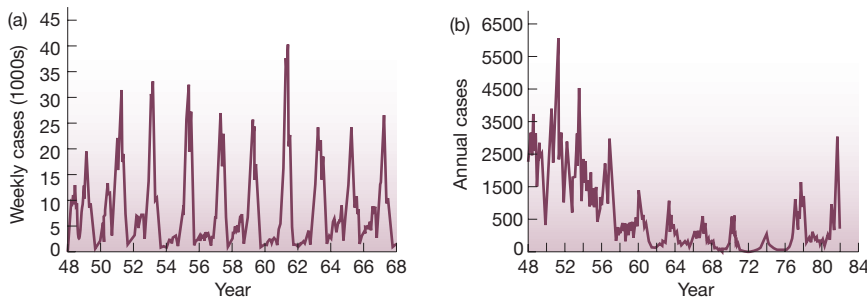
Putting it simply, for microparasites with direct transmission, the basic reproductive rate,  $R_0$ , measures the average number of new infections arising from a single infected individual in a population of susceptible hosts. It increases with the average period of time over which an infected host remains infectious,  $L$ , since a long infectious period means plenty of opportunity to transmit to new hosts; it increases with the number of susceptible individuals in the host population,  $S$ , because more susceptible hosts offer more opportunities ('targets') for transmission of the parasite; and it increases with the transmission rate of the infection,  $\beta$ , because this itself increases first with the infectiousness of the parasite – the probability that contact leads to transmission – but also with the likelihood of infectious and susceptible hosts coming into contact as a reflection of the pattern of host behavior (Anderson, 1982). Thus, overall:

$$R_0 = S \cdot \beta L$$

We know that  $R_0 = 1$  is a transmission threshold, in that below this the infection will die out but above it the infection will spread. But this in turn allows us to define a critical *threshold population size*  $S_T$ : the number of susceptibles that give rise to  $R_0 < 1$ . At that threshold, making  $R_0 = 1$  in the equation means:

$$S_T = 1/\beta L$$

In populations with fewer susceptibles than this, the infection will die out ( $R_0 < 1$ ), but with more than this, the infection will spread ( $R_0 > 1$ ). The threshold population size is larger (more individuals are required to sustain an infection) when infectiousness ( $\beta$ ) is low and/or infections themselves are short-lived (small  $L$ ).

**Figure 7.20**

(a) Reported cases of measles in England and Wales from 1948 to 1968, prior to the introduction of mass vaccination. (b) Reported cases of pertussis (whooping cough) in England and Wales from 1948 to 1982. Mass vaccination was introduced in 1956.

20th century. Current estimates suggest that around 900,000 deaths occur each year from measles infection in the developing world (Walsh, 1983).

Moreover, the immunity induced by many bacterial and viral infections, combined with death from the infection, reduces the number of susceptibles in a population, reduces  $R_0$ , and therefore tends to lead to a decline in the incidence of the disease itself. In due course, though, there will be an influx of new susceptibles into the population (as a result of new births or perhaps immigration), an increase in  $R_0$ , an increase in incidence, and so on. There is thus a marked tendency with such diseases to generate a sequence from ‘high incidence’, to ‘few susceptibles’, to ‘low incidence’, to ‘many susceptibles’, to ‘high incidence’, etc. – just like any other predator–prey cycle. This undoubtedly underlies the observed cyclic incidence of many human diseases (especially prior to modern immunization programs), with the differing lengths of cycle reflecting the differing characteristics of the diseases: measles with peaks every 1 or 2 years, pertussis (whooping cough) every 3–4 years, diphtheria every 4–6 years, and so on (Figure 7.20).

### 7.5.4 Crowding

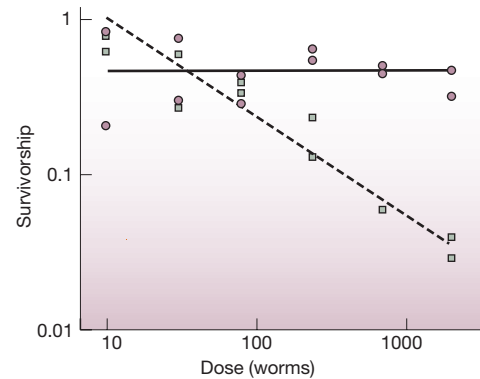
One fundamental feature that we have ignored so far is the fact that no predator lives in isolation: all are affected by other predators. The most obvious effects are competitive; many predators compete, and this results in a reduction in the consumption rate per individual as predator density increases (see Chapter 3). However, even when food is not limited, the consumption rate per individual can be reduced by increases in predator density by a number of processes known collectively as ‘mutual interference’. For example, many predators interact behaviorally with other members of their population, leaving less time for feeding. Humming-birds actively and aggressively defend rich sources of nectar; parasitoid wasps will threaten and, if need be, fiercely drive away an intruder from their own area of tree trunk. Alternatively, an increase in consumer density may lead to an increased rate of emigration, or of consumers stealing food from one another (as do many gulls), or the prey themselves may respond to the presence of consumers and become less available for capture.

In all such cases, the underlying pattern is the same: the consumption rate per individual predator declines with increasing predator density. This reduction is likely to have an adverse effect on the fecundity, growth and mortality of individual predators, which intensifies as predator density increases. The predator population is thus subject to density-dependent regulation (see Chapters 3 and 5).

mutual interference amongst predators reduces the predation rate

**Figure 7.21**

Host immune responses are necessary for density dependence in infections of the rat with the nematode *Strongyloides ratti*. Survivorship is independent of initial dose in mutant rats without an immune response (●; slope not significantly different from 0), but with an immune response (■) it declines (slope =  $-0.62$ , significantly less than 0;  $P < 0.001$ ).



AFTER PATERSON &amp; VINEY, 2002

competition or the immune response in parasites?

With parasites, too, it is to be expected that individuals will often interfere with each other's activities, and that there will be intraspecific competition between parasites and density dependence in their growth, birth and/or death rates. However, for vertebrate hosts at least, we need to remember that the intensity of the immune reaction elicited from a host also typically depends on the abundance of parasites. A rare attempt to disentangle these two effects utilized the availability of mutant rats lacking an effective immune response (Figure 7.21). These and normal, control rats were subjected to experimental infection with a nematode, *Strongyloides ratti*, at a range of doses. Any reduction in parasite fitness with dose in the normal rats could be due to intraspecific competition and/or an immune response that itself increases with dose; but clearly, in the mutant rats only the first of these is possible. In fact, there was no observable response in the mutant rats (Figure 7.21), indicating that at these doses, which were themselves similar to those observed naturally, there was no evidence of intraspecific competition, and that the pattern observed in the normal rats is entirely the result of a density-dependent immune response. Of course, this does not mean that there is never intraspecific competition amongst parasites within hosts, but it does emphasize the particular subtleties that arise when an organism's habitat is its reactive host.

Moreover, it is, of course, not only the predators that may be subject to the effects of crowding. Prey, too, are likely to suffer reductions in growth, birth and survival rates as their abundance increases and their individual intake of resources declines.

crowding tends to dampen or eliminate predator–prey cycles

The effect of either predator or prey crowding on their dynamics is, in a general sense, fairly easy to predict. Prey crowding prevents their abundance from reaching as high a level as it would otherwise do, which means in turn that predator abundance is also unlikely to reach the same peaks. Predator crowding, similarly, prevents predator abundance from rising so high, but also tends to prevent them from reducing prey abundance as much as they would otherwise do. Overall, therefore, crowding is likely to have a damping effect on any predator–prey cycles, reducing their amplitude or removing them altogether; not just because crowding chops off the peaks and troughs, but also because each peak in a cycle tends itself to generate the next trough (e.g. high prey abundance → high predator abundance → low prey abundance), so that the lowering of peaks in itself tends to raise troughs.

There are certainly examples that appear to confirm the stabilizing effects of crowding in predator–prey interactions. For instance, there are two groups of primarily herbivorous rodents that are widespread in the Arctic: the microtine rodents (lemmings and voles) and the ground squirrels. The microtines are renowned for their dramatic, cyclic fluctuations in abundance, but the ground squirrels have populations that remain remarkably constant from year to year, especially in open meadow and tundra habitats. There, significantly, they appear to be strongly self-limited by food availability, suitable burrowing habitat and their own spacing behavior (Karels & Boonstra, 2000).

### 7.5.5 Predators and prey in patches

The second feature that was ignored initially but will be examined here is the fact that many populations of predators and prey exist not as a single, homogeneous mass, but as a *metapopulation* – an overall population divided, by the patchiness of the environment, into a series of subpopulations, each with its own internal dynamics but linked to other subpopulations by movement (dispersal) between patches (a topic developed further in Section 9.3).

It is possible to get a good idea of the general effect of this spatial structure on predator–prey dynamics by considering the simplest imaginable metapopulation: one consisting of just two subpopulations. If the patches are displaying the same dynamics, and dispersal is the same in both directions, then the dynamics are unaffected: every ‘lost’ individual is counteracted by an equivalent gain. To put it simply, patchiness and dispersal have no effect in their own right. Differences between the patches, however, either in the dynamics within subpopulations or in the dispersal between them, tend, in themselves, to stabilize the interaction: to dampen any cycles that might exist. The reason is that any difference leads to asynchrony in the fluctuations in the patches. Inevitably, therefore, a population at the peak of its cycle tends to lose more by dispersal than it gains, a population at a trough tends to gain more than it loses, and so on. In addition, even with just two patches, if one subpopulation goes extinct, the other (asynchronous) subpopulation is unlikely to do so at the same time. Dispersers from it may therefore ‘rescue’ the first, allowing the population as a whole, the metapopulation, to persist. Dispersal and asynchrony together, therefore – and some degree of asynchrony is likely to be the general rule – tend to dampen fluctuations in predator–prey dynamics and make population persistence more likely.

Is it possible, though, to see the stabilizing influence of this type of metapopulation structure in practice? One famous example is experimental work on a laboratory system in which a predatory mite *Typhlodromus occidentalis* fed on a herbivorous mite *Eotetranychus sexmaculatus*, which fed on oranges interspersed amongst rubber balls in a tray. In the absence of its predator, *Eotetranychus* maintained a fluctuating but persistent population (Figure 7.22a). However, if *Typhlodromus* was added during the early stages of prey population growth, it rapidly increased its own population size, consumed all of its prey and then became extinct itself (Figure 7.22b): the underlying predator–prey dynamics were unstable.

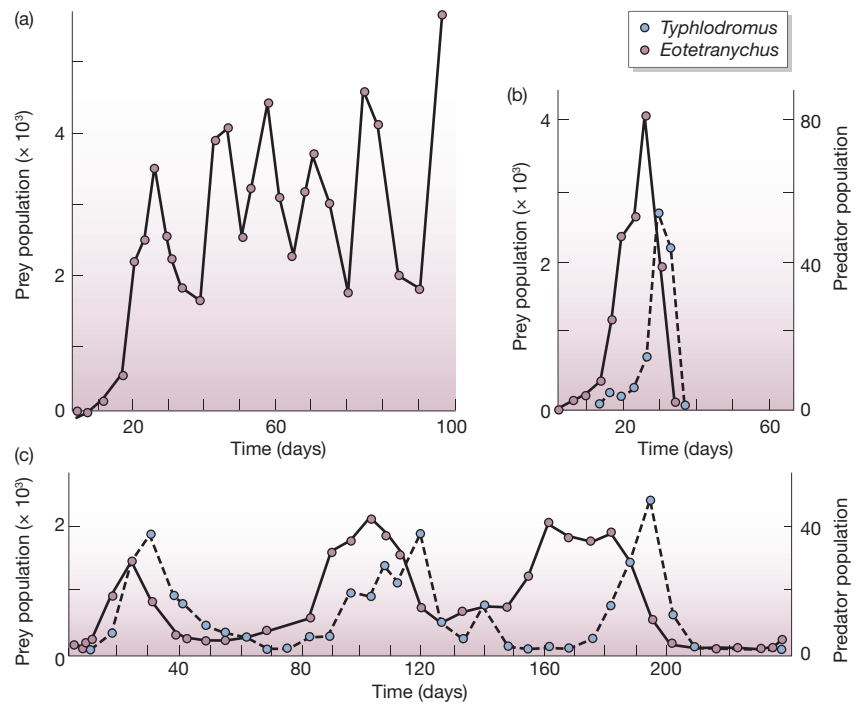
The interaction was altered, however, when the habitat was made more ‘patchy’. The oranges were spread further apart and partially isolated from each other by placing a complex arrangement of petroleum jelly barriers in the tray,

dispersal and asynchrony  
dampen cycles

stabilizing metapopulation effects  
in Huffaker’s mites . . .

**Figure 7.22**

Predator–prey interactions between the mite *Eotetranychus sexmaculatus* and its predator, the mite *Typhlodromus occidentalis*. (a) Population fluctuations of *Eotetranychus* without its predator. (b) A single oscillation of the predator and prey in a simple system. (c) Sustained oscillations in a more complex system.



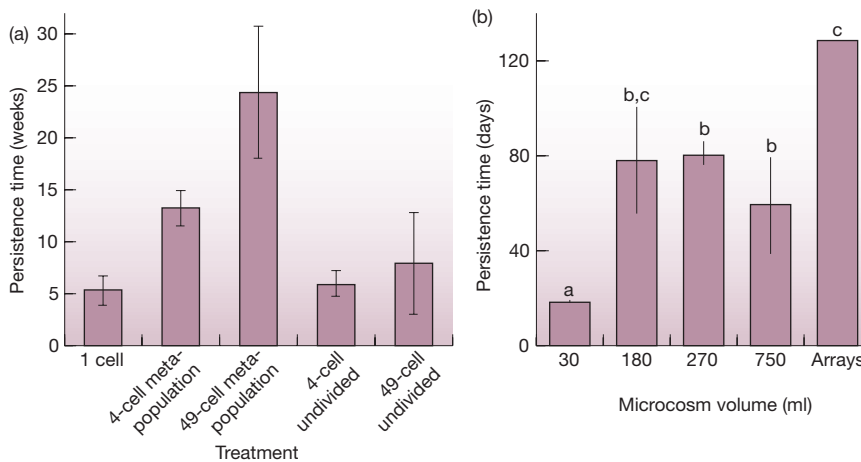
AFTER HUFFAKER, 1958

which the mites could not cross. The dispersal of *Eotetranychus* was facilitated, however, by inserting a number of upright sticks from which they could launch themselves on silken strands carried by air currents. Dispersal between patches was therefore much easier for prey than it was for predators. In a patch occupied by both, the predators consumed all the prey and then either became extinct themselves or dispersed (with a low rate of success) to a new patch. In patches occupied by prey alone, there was rapid, unhampered growth accompanied by successful dispersal to new patches. And in a patch occupied by predators alone, there was usually death of the predators before their food arrived. Predators and prey were therefore ultimately doomed to extinction in each patch – that is, the patch dynamics were unstable. But overall, at any one time, there was a mosaic of unoccupied patches, prey–predator patches heading for extinction, and thriving prey patches; and this mosaic was capable of maintaining persistent populations of both predators and prey (Figure 7.22c).

... and in starfish and mussels

A similar example, from a natural population, is provided by work off the coast of southern California on the predation by starfish of clumps of mussels (Murdoch & Stewart-Oaten, 1975). Clumps that are heavily preyed upon are liable to be dislodged by heavy seas so that the mussels die; the starfish are continually driving patches of their mussel prey to extinction. The mussels, however, have planktonic larvae that are continually colonizing new locations and initiating new clumps, whereas the starfish disperse much less readily. They aggregate at the larger clumps, but there is a time lag before they leave an area when the food is gone. Thus, patches of mussels are continually becoming extinct, but other clumps are growing prior to the arrival of the starfish.





**Figure 7.23**

A metapopulation structure can increase the persistence of predator–prey interactions. (a) The parasitoid, *Anisopteromalus calandrae*, attacking its bruchid beetle host, *Callosobruchus chinensis*, lived on beans either in small single ‘cells’ (short persistence time, left), or in combinations of cells (4 or 49), which either had free access between them so that they effectively constituted a single population (persistence time not significantly increased, right), or had limited (infrequent) movement between cells so that they constituted a metapopulation of separate subpopulations (increased persistence time, center). Bars are standard errors. (b) The predatory ciliate, *Didinium nasutum*, feeding on the bacterivorous ciliate, *Colpidium striatum*, in bottles of various volumes (30–750 ml), where persistence time varied little, except in the smallest populations (30 ml) where times were shorter, and also in ‘arrays’ of 9 or 25 linked 30 ml bottles (metapopulations), where persistence was greatly prolonged: all populations persisted until the end of the experiment (130 days). Bars are standard errors; different letters above bars indicate treatments that were significantly different from one another ( $P < 0.05$ ).

As with the mites, the combination of patchiness, the aggregation of predators in particular patches, and a lack of synchrony between the behavior of different patches appears capable of stabilizing the dynamics of a predator–prey interaction.

Others, too, have demonstrated the power of a metapopulation structure in promoting the persistence of coupled predator and prey populations when their dynamics in individual subpopulations are unstable. Figure 7.23a, for example, shows this for a parasitoid attacking its beetle host. Figure 7.23b shows similar results for prey and predatory ciliates (protists), where, in support of the role of a metapopulation structure, it was also possible to demonstrate the asynchrony in the dynamics of individual subpopulations and frequent local prey extinctions and recolonizations (Holyoak & Lawler, 1996).

A metapopulation structure, then, like crowding, can have an important influence on predator–prey dynamics. More generally, however, the message from this section is that predator–prey dynamics can take a wide variety of forms, but there are good grounds for believing that we can make sense of this variety through seeing it as a reflection of the way in which the different aspects of predator–prey interactions combine to play out variations on an underlying theme.

metapopulation effects in mites and ciliates

an explanation for the variety of predator–prey dynamics begins to emerge

## 7.6 Predation and community structure

What roles can predation play when we broaden our perspective from populations to whole ecological communities? Central to this is the notion that predation, in many of its effects, is just one of the forces acting on communities that can be described as a ‘disturbance’. For example, the result of a predator opening up a gap in a community for colonization by other organisms is often indistinguishable from that of battering by waves on a rocky shore or a hurricane in a forest.

In fact, many of the effects of predation (and other disturbances) on community structure are the result of its interaction with competitive exclusion (taking up a theme introduced in Section 6.2.8). In an undisturbed world, the most competitive species might be expected to drive less competitive species to extinction. However, this assumes first that the organisms are actually competing. Yet there are many situations where predation may hold down the densities of competitors, so that resources are not limiting and individuals do not compete for them. When predation promotes the coexistence of species that might otherwise exclude one another, this is known as *predator-mediated coexistence*.

For example, in a study of nine Scandinavian islands, pigmy owls (*Glaucidium passerinum*) occurred on only four of the islands, and the pattern of occurrence of three species of tit had a striking relationship with this distribution. The five islands without the predatory owl were home to only one species, the coal tit (*Parus ater*). However, in the presence of the owl, the coal tit was always joined by two larger tit species, the willow tit (*P. montanus*) and the crested tit (*P. cristatus*). Kullberg and Ekman (2000) argue that the coal tit is the superior competitor for food; but the two larger species are less affected than the coal tit by predation from the owl. It seems that the owl may be responsible for predator-mediated coexistence, by reducing the competitive dominance enjoyed by coal tits in its absence.

In another example, grazing by local zebu cattle in natural pasture in the Ethiopian highlands was manipulated to provide a no-grazing control and four grazing intensity treatments in two sites. Figure 7.24 shows how the mean

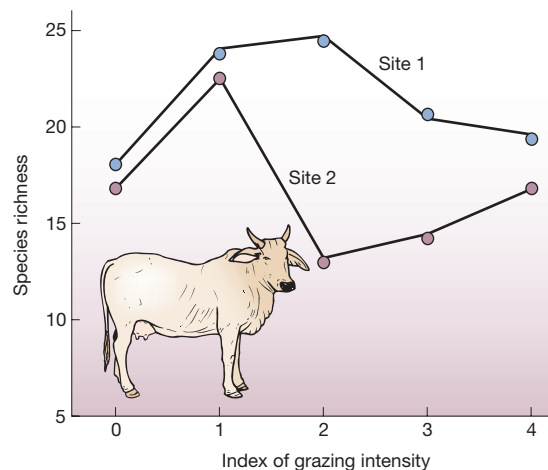
predation as an interruptor  
of competitive exclusion:  
predator-mediated coexistence

owls and tits on Scandinavian  
islands

grazing by cattle can promote  
the coexistence of plants

**Figure 7.24**

Mean species richness of pasture vegetation in plots subjected to different levels of cattle grazing in two sites in the Ethiopian highlands in October. 0, no grazing; 1, light grazing; 2, moderate grazing; 3, heavy grazing; 4, very heavy grazing (estimated according to cattle stocking rates).



number of plant species varied in the sites in October, the period when plant productivity was at its highest. Significantly more species occurred at intermediate levels of grazing than where there was no grazing or heavier grazing ( $P < 0.05$ ).

In the ungrazed plots, several highly competitive plant species, including the grass *Bothriochloa insculpta*, accounted for 75–90% of ground cover. At intermediate levels of grazing, however, the cattle kept the dominant grasses in check and allowed a greater number of plant species to persist. But at very high intensities of grazing, cattle were forced to turn to less preferred species, driving some to extinction and allowing grazing-tolerant species such as *Cynodon dactylon* to become dominant, so that plant species numbers were again reduced (Figure 7.24). Overall, the number of species was greatest at intermediate levels of predation.

This suggests that, as a generalization, *selective* predation should favor an increase in species numbers in a community as long as the preferred prey are competitively dominant, although species numbers may also be low at very high predation pressures. To take another example, along the rocky shores of New England, the most abundant and important herbivore in mid and low intertidal zones is the periwinkle snail *Littorina littorea*. The snail will feed on a wide range of algal species but is relatively selective: it shows a strong preference for small, tender species and in particular for the green alga *Enteromorpha intestinalis*. The least-preferred foods are much tougher (e.g. the perennial red alga *Chondrus crispus* and brown algae).

Is *Enteromorpha*, the periwinkles' preferred food, a competitive dominant in their absence? Naturally, in a *Chondrus* pool, periwinkles feed on the young stages of many ephemeral algae that settle on *Chondrus*, including *Enteromorpha*. However, if periwinkles are artificially removed from a *Chondrus* pool, *Enteromorpha* and several other algae settle, grow and become abundant. *Enteromorpha* achieves competitive dominance, while *Chondrus* becomes bleached and then disappears. Conversely, adding periwinkles to *Enteromorpha* pools leads, in a year, to a decline in the percentage cover of *Enteromorpha* from almost 100% to less than 5%, as *Chondrus* colonizes and eventually comes to dominate. Clearly, periwinkles are responsible for the dominance of *Chondrus* in *Chondrus* pools.

The natural composition of tide pools in the rocky intertidal varies from almost pure stands of *Enteromorpha* to almost pure stands of *Chondrus*. Is grazing by the periwinkle responsible? A survey suggests that it is (Figure 7.25a). When periwinkles were absent or rare, *Enteromorpha* appeared to competitively exclude other species and the number of algal species was low. At very high densities of periwinkles, however, all palatable algal species were consumed to extinction, leaving almost pure stands of *Chondrus*. As with the cattle, therefore, it was at intermediate predation intensities that the abundance of *Enteromorpha* and other ephemeral algal species was reduced, competitive exclusion was prevented, and many species, both palatable and unpalatable, coexisted.

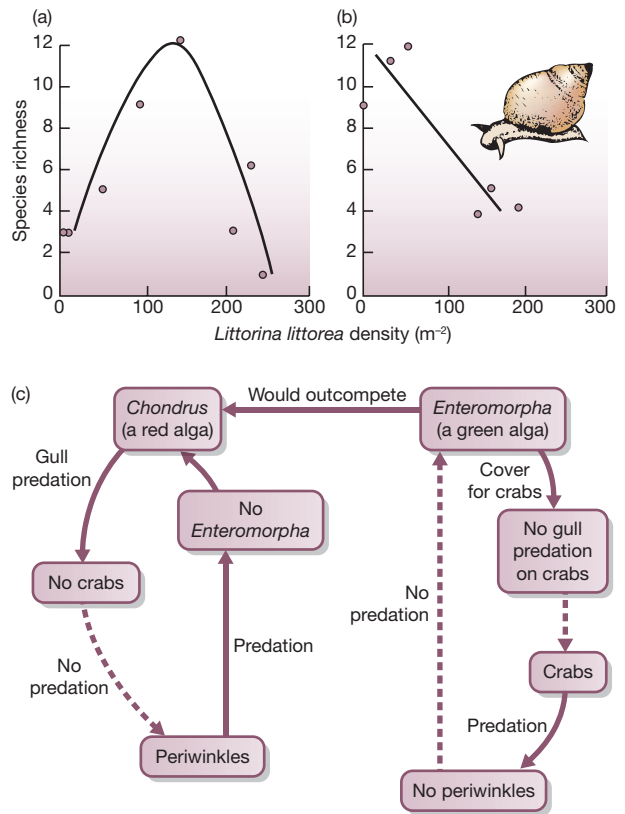
Why then do some pools contain periwinkles while others do not? Predation is again the answer. The periwinkle colonizes pools in its immature, planktonic stage. Planktonic periwinkles are just as likely to settle in *Enteromorpha* pools as *Chondrus* pools, but the crab *Carcinus maenas*, which can shelter in the

do most species occur at intermediate levels of predation?

selective predation on a rocky shore

**Figure 7.25**

The effect of *Littorina littorea* (periwinkle) density on species richness (a) in tide pools and (b) on emergent substrata. (c) The web of interactions giving rise to the relationship in tide pools shown in (a).



(a, b) AFTER LUBCHENCO, 1978

*Enteromorpha* canopy, feeds on the young periwinkles and prevents them from establishing. The final thread in this tangled web of predator–prey interactions is the effect of gulls, which prey on crabs where the dense green algal canopy is absent. Thus there is no bar to continuing periwinkle recruitment in *Chondrus* pools. These relationships, and the key roles of predation, are summarized in Figure 7.25c.

The picture is quite different, though, when the preferred prey species is not competitively dominant. Here, increased predation pressure should simply reduce the number of prey species in the community. This can also be illustrated on the rocky shores of New England, where the competitive dominance of the plants is more evenly balanced when they interact on emergent substrata rather than in tide pools. Any increase in the predation pressure, therefore, simply decreases the algal diversity, as the preferred, ephemeral species like *Enteromorpha* are consumed totally and prevented from re-establishing themselves (Figure 7.25b).

Overall, then, predation can have an important role in developing our understanding of the structure of ecological communities, not least in reminding us that the patterns we saw in Chapter 6 when we were focusing on interspecific competition may never get a chance to express themselves because communities in the real world rarely proceed smoothly to an equilibrium state.



## Summary

# SUMMARY

### Predation, true predators, grazers and parasites

A predator may be defined as any organism that consumes all or part of another living organism (its 'prey' or 'host') thereby benefiting itself, but, under at least some circumstances, reducing the growth, fecundity or survival of the prey.

'True' predators invariably kill their prey and do so more or less immediately after attacking them, and consume several or many prey items in the course of their life. Grazers also attack several or many prey items in the course of their life, but consume only part of each prey item and do not usually kill their prey. Parasites also consume only part of each host, and also do not usually kill their host, especially in the short term, but attack one or very few hosts in the course of their life, with which they therefore often form a relatively intimate association.

### The subtleties of predation

Grazers and parasites, in particular, often exert their harm not by killing their prey immediately like true predators, but by making the prey more vulnerable to some other form of mortality.

The effects of grazers and parasites on the organisms they attack are often less profound than they first seem because individual plants can compensate for the effects of herbivory and hosts may have defensive responses to attack by parasites.

The effects of predation on a population of prey are complex to predict because the surviving prey may experience reduced competition for a limiting resource, or produce more offspring, or other predators may take fewer of the prey.

### Predator behavior

True predators and grazers typically 'forage', moving around within their habitat in search of their prey. Other predators 'sit and wait' for their prey, though almost always in a selected location. With parasites and pathogens there may be direct transmission between infectious and uninfected hosts, or contact between free-living stages of the parasite and uninfected hosts may be important.

Optimal foraging theory aims to understand why particular patterns of foraging behavior have been

favoured by natural selection (because they give rise to the highest net rate of energy intake).

Generalist predators spend relatively little time searching but include relatively low-profitability items in their diet. Specialists only include high-profitability items in their diet but spend a relatively large amount of their time searching for them.

### Population dynamics of predation

There is an underlying tendency for predators and prey to exhibit cycles in abundance, and cycles are observed in some predator-prey and host-parasite interactions. However, there are many important factors that can modify or override the tendency to cycle.

Crowding of either predator or prey is likely to have a damping effect on any predator-prey cycles.

Many populations of predators and prey exist as a 'metapopulation'. In theory, and in practice, asynchrony in population dynamics in different patches and the process of dispersal tend to dampen any underlying population cycles.

### Predation and community structure

There are many situations where predation may hold down the densities of populations, so that resources are not limiting and individuals do not compete for them. When predation promotes the coexistence of species amongst which there would otherwise be competitive exclusion (because the densities of some or all of the species are reduced to levels at which competition is relatively unimportant) this is known as 'predator-mediated coexistence'.

The effects of predation generally on a group of competing species depend on which species suffers most. If it is a subordinate species, then this may be driven to extinction and the total number of species in the community will decline. If it is the competitive dominants that suffer most, however, the results of heavy predation will usually be to free space and resources for other species, and species numbers may then increase.

It is not unusual for the number of species in a community to be greatest at intermediate levels of predation.

## Review questions

### REVIEW QUESTIONS

Asterisks indicate challenge questions

- 1 With the aid of examples, explain the feeding characteristics of true predators, grazers, parasites and parasitoids.
- 2\* True predators, grazers and parasites can alter the outcome of competitive interactions that involve their 'prey' populations: discuss this assertion using one example from each category.
- 3 Discuss the various ways that plants may 'compensate' for the effects of herbivory.
- 4 Predation is 'bad' for the prey that get eaten. Explain why it may be good for those that do not get eaten.
- 5\* Discuss the pros and cons, in energetic terms, of (i) being a generalist as opposed to a specialist predator, and (ii) being a sit-and-wait predator as opposed to an active forager.
- 6 In simple terms, explain why there is an underlying tendency for populations of predators and prey to cycle.
- 7\* You have data that shows cycles in nature among interacting populations of a true predator, a grazer and a plant. Describe an experimental protocol to determine whether this is a grazer–plant cycle or a predator–grazer cycle.
- 8 Define mutual interference and give examples for true predators and parasites. Explain how mutual interference may dampen inherent population cycles.
- 9 Discuss the evidence presented in this chapter that suggests environmental patchiness has an important influence on predator–prey population dynamics.
- 10 With the help of an example, explain why most prey species may be found in communities subject to an intermediate intensity of predation.



# Chapter 8



## Evolutionary ecology

### *Chapter contents*

#### CHAPTER CONTENTS

- 8.1 Introduction
- 8.2 Molecular ecology: differentiation within and between species
- 8.3 Coevolutionary arms races
- 8.4 Mutualistic interactions

### *Key concepts*

#### KEY CONCEPTS

In this chapter you will:

- appreciate the range of molecular (DNA) markers that have been used in ecology
- understand how these markers can be put to work in determining the extent of subdivision within, and the degree of separation between, species
- recognize the importance of coevolutionary arms races in the dynamics of the component populations, especially of plants and their insect herbivores, and of parasites and their hosts
- understand the nature of mutualistic interactions in general and their crucial importance both for the species concerned and for almost all communities on the planet
- appreciate the particular contributions of mutualisms in diverse areas from farming, through the functioning of guts and roots, to the fixation of nitrogen by plants

*We have noted previously that nothing in ecology makes sense, except in the light of evolution. But some areas of ecology are even more evolutionary than others. We may need to look within individuals to examine the details of the genes they carry, or to acknowledge explicitly the crucial and reciprocal role that species play in one another's evolution.*

## 8.1 Introduction

In Chapter 2, we set the scene for the remainder of this book by illustrating how, to modify slightly Dobzhansky's famous phrase, 'nothing in ecology makes sense, except in the light of evolution'. But evolution does more than underpin ecology (and the whole of the rest of biology). There are many areas in ecology where evolutionary adaptation by natural selection takes center stage to the extent that the term 'evolutionary ecology' is often used to describe them. In several previous chapters, therefore, topics in evolutionary ecology have been dealt with, quite naturally, as integral parts of broader ecological questions. In Chapter 3, we examined the nature and importance of defenses that have evolved to protect plants and prey from their predators. In Chapter 5, we saw how patterns in life histories – schedules of growth, reproduction and so on – can only be understood in relation to corresponding patterns in the habitats in which they have evolved. In Chapter 6, we looked at interspecific competition as an evolutionary driving force, generating patterns in the coexistence and exclusion of competing species. And in Chapter 7, we discussed 'optimal foraging': the evolution of behavioral strategies that maximize predator fitness and thus mold their dynamic interactions with their prey.

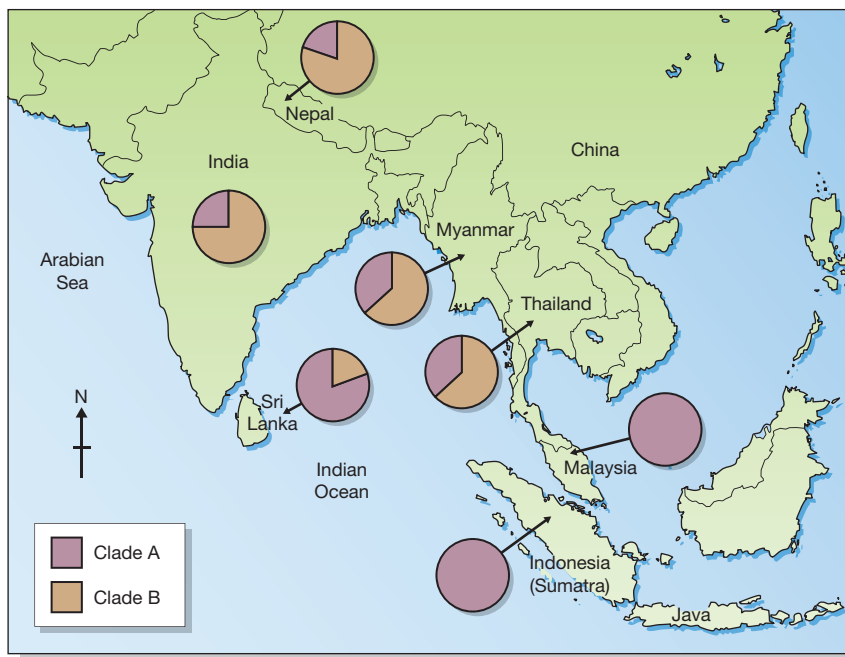
This, of course, is not an exhaustive survey of topics in evolutionary ecology. In the present chapter, therefore, we deal with a number of others (though the final list will remain less than exhaustive). We focus especially on *coevolution*: pairs of species acting as reciprocal driving forces in one another's evolution. The question of coevolutionary 'arms races' between predators and their prey is taken up in Section 8.3, with a particular emphasis on host–pathogen interactions: each adaptation in the prey that fends off or avoids the attacks of a predator provoking a corresponding adaptation in the predator that improves its ability to overcome those defenses. However, not all coevolutionary interactions are antagonistic. Many species-pairs are 'mutualists': both parties benefiting, on balance at least, from the interactions in which they take part. Some of the most important of these mutualisms – pollination, corals and nitrogen fixation, for example – are discussed in Section 8.4. We begin, though, not with species interactions but with aspects of evolutionary differentiation within and between species, especially those detectable by modern techniques developed in molecular genetics and thus often described as aspects of 'molecular ecology'.

## 8.2 Molecular ecology: differentiation within and between species

For much of the time, it is entirely appropriate for ecologists to talk about ‘populations’ or ‘species’ as if they were singular, homogeneous entities: for example, we may talk of ‘the distribution of Asian elephants’, saying nothing about whether the species might be differentiated into distinct races or subgroups, as indeed it is (Figure 8.1). But for some purposes, knowing how much differentiation there is within species, or between one species and another, is critical for an understanding of their dynamics, and ultimately for managing those dynamics. Is a particular population derived largely from offspring born locally, or from immigrants from another, distinguishable population? Where exactly does the distribution of a particular species end and that of another, closely related species begin? In cases like these, being able to determine, at a variety of scales, who is most closely related to whom (and who is quite distinct from whom) may be essential.

Our ability to do this itself depends on the resolution with which we can differentiate individuals from one another and even determine where they came from or who their parents were. In the past, this was difficult and frequently impossible: reliance on simple, visual markers meant that all individuals within a species often looked the same, and even members of closely related species could often only be distinguished by experienced taxonomists looking down a microscope at, say, details of a male’s genitalia. Now, though, molecular, genetic markers (albeit still requiring experts and expensive equipment) have massively

the need to know who is most closely related to whom



**Figure 8.1**

Distribution of two distinct ‘clades’ of the Asian elephant, *Elephas maximus* (groups with distinct evolutionary histories following their common origin), revealed only by an analysis of molecular markers. These clades coexist in many areas, though their distinctiveness itself suggests a degree of independence in their dynamics even when they do coexist.

increased the resolution at which we can differentiate between populations and even between individuals, and hence have vastly improved our ability to address these types of questions. We begin, therefore, in Box 8.1, with a brief survey of some of the most important of these molecular markers and their uses.



## 8.1 QUANTITATIVE ASPECTS

### 8.1 *Quantitative aspects*

#### Molecular markers

This is not the place for crash courses in either molecular biology or the laboratory methods used to extract, amplify, separate and analyze molecular markers, but it will nonetheless be useful to have some appreciation of their nature and key properties – and to be introduced to some of the technical terms and abbreviations that abound in this area. Most recent studies in ecology have used DNA of one type or other for molecular identification. We need, at the very least, to be aware that a length of DNA is characterized by the sequence of bases of which it is composed, adenine (A), cytosine (C), guanine (G) and thymine (T), and that in double-stranded DNA, these link across to one another in complementary base-pairs: A-T and G-C.

#### Choosing a molecular marker

The basis for all uses of molecular markers in ecology is that individuals can be differentiated from one another to greater or lesser extents as a result of molecular variation amongst them. The ultimate source of this variation is mutation in the sequence of bases, which, of course, occurs independently of its consequences for the organism concerned. What happens to the mutation, and the mutated organism, then depends essentially on the balance between selection and ‘genetic drift’ (random, undirected changes in gene frequency from generation to generation). If the mutation occurs in a region of DNA that is important because, say, it codes for a crucial part of an essential enzyme, then selection is likely to determine the outcome. An unfavorable mutation (the vast majority in important regions of DNA) will quickly be lost because the mutated organism is less fit than its

counterparts. Individuals will therefore differ relatively little in such regions, and if they do, differentiation is most likely to reflect ‘adaptive’ variation: different variants being favored in different individuals, perhaps because of where they live.

But there are also regions of DNA that appear not to code for important parts of enzymes or to perform any other function where the precise sequence is crucial. Variation in these regions is therefore said to be ‘neutral’, and mutations can accumulate there over time. Imagine two offspring of a single mating. They will be genetically very similar. But imagine now that each, literally, goes its own way. As each generation passes and mutations accumulate, the lineages derived from them will become increasingly divergent in those regions of their genome where variation is neutral, and lineages derived from those lineages will diverge in their turn. A snapshot taken in the future should allow us to determine, broadly, who has diverged most recently, and which groups have barely diverged at all, though our ability to do this will itself depend on the rate of mutation in the DNA region concerned: too slow and individuals will tend all to look the same; too fast and each individual sampled will tend to be so unique that its relationships to others will be hard to discern. Molecular markers are therefore chosen, ideally, such that the mutation rate matches the question being addressed. A study of differentiation between gerbils living in different burrow systems in the same, local population should use a region of DNA where the mutation rate is high (much divergence from generation to generation); whereas a study tracing the routes of colonization that have placed different populations of brown bears

over the whole of Europe in the 10,000–12,000 years since the last glaciation should use a region where the mutation rate is relatively low.

### Polymerase chain reaction (PCR)

As a practical point, most studies in molecular ecology, having extracted the DNA from the organism concerned, use the polymerase chain reaction (PCR) to amplify the amount of target material such that there is sufficient available for analysis. By therefore being able to make use of small samples, this has revolutionized our ability to sample individuals ‘non-invasively’, using blood, hair, feces or wing clips. Very simply, PCR requires ‘primers’ that flank the particular sequence of DNA that is to be amplified. In the PCR reaction, nowadays fully automated, the originally double-stranded DNA is denatured to single strands, the primers anneal to the separated strands, and an enzyme, DNA polymerase, copies the sequence between the primers. This series of reactions is then repeated 30–40 times, and, since the process of repeated amplification is exponential, an originally small amount of target DNA in the midst of other, unwanted sequences becomes a large enough amount of target to be subjected to analysis. Note, though, that hidden within this brief description is the need to have identified not only informative target regions of DNA, but also the primers that characterize them.

### Nuclear and mitochondrial DNA

In the past especially, many studies have used not nuclear DNA (inherited equally from both parents and holding the code for the vast majority of an organism’s functions) but the relatively small lengths of mitochondrial DNA (mtDNA), found in the mitochondria in the cytoplasm of each of an organism’s cells. The main advantages of mtDNA are that, almost always, it is inherited only from the mother (who contributes the cytoplasm to the fused egg) and does not undergo recombination. Thus, lineages can be more clearly traced from generation to generation. Also, the mutation rate is higher than for coding regions of nuclear DNA, allowing finer resolution differentiation. On the other hand, mtDNA offers only a small number of targets, and its maternal inheritance means that when disparate types meet in a population it is impossible to know whether any individuals are the result of

matings between them. Increasingly, therefore, studies are focusing on regions of nuclear DNA, though often in parallel with analyses of mtDNA genes, combining the advantages of both.

### Microsatellites

Within the nuclear genome, sequences coding for proteins (i.e. genes) are by no means the only regions that have been utilized by molecular biologists. Microsatellites, for example, are regions of DNA in which the same two, three or four bases are repeated many times, preceded and followed in the sequence by flanking regions that uniquely identify each microsatellite (Figure 8.2a). The variability comes from the fact that the number of ‘repeats’ can vary, the resulting lengths of microsatellite DNA being measured by the speed at which they move through a semisolid medium (a ‘gel’) under the influence of an electric current (electrophoresis). Microsatellites may be highly polymorphic within a population. Thus, an appropriately chosen ‘panel’ of microsatellites for a species may effectively allow each individual in a population to be uniquely identified (a DNA ‘fingerprint’), making microsatellites especially appropriate at the finer scales of differentiation.

### Sequencing

As far as nuclear or mitochondrial genes are concerned, having chosen, extracted and amplified the target region from a sample of individuals, it is necessary to have some basis for differentiating individuals from one another, determining who is most similar to whom, and so on. Increasingly, as automation improves, and costs come down, the whole sequences of genes are being determined. As previously noted, regions of the same gene differ in terms of their functional importance (Figure 8.2b). Some regions are ‘conserved’ from individual to individual, from population to population, and often from species to species. These are (or are presumed to be) the regions of greatest functional importance, and they play effectively no part in differentiation. But there are other regions where far more variation is observed (and that can be presumed, therefore, to be neutral or at least subject to weaker selective constraints), and it is on the basis of this that individuals and populations can be differentiated.

### Figure 8.2

(a) A 'locus', here, refers to the location of a region in the overall DNA sequence. An 'allele' is the particular variant of sequence that exists at that locus in a particular case. Remember that that sequence is of *two* strands of DNA, between which the bases are paired: G with C and A with T. This figure shows two contrasting alleles at a microsatellite locus, with its sequence of repeated bases (of differing length) in the two DNA strands (red) and exactly similar flanking regions at either end (black). (b) This figure, by contrast, shows the base sequence in just one DNA strand of a hypothetical gene (i.e. a sequence of DNA coding for a protein) from five individuals. Note the contrast between the conserved (unvarying) regions at either end, in black, and a variable region in red towards the center. Differentiation between individuals clearly depends on this variable region.

(a)

Allele 1 which has 10 repeats

...GCATTGCGATAAAG**TGTGTGTGTGTGTGTGTGTGCCATGCCGGATGA**...

...CGTAACGCTATTGC**ACACACACACACACACAC**GGTACGGCCTACT...

Flanking region                      Microsatellite                      Flanking region

Allele 2 which has 8 repeats

...GCATTGCGATAACG**TGTGTGTGTGTGTGCCATGCCGGATGA**...

...CGTAACGCTATTGC**ACACACACACACAC**GGTACGGCCTACT...

(b)

Individual 1. ...CGTAACGCTATTGCGC**ATTGTGATAACAC**CATGCCGGATGA...

Individual 2. ...CGTAACGCTATTGCGC**CATCCGATCATAT**CATGCCGGATGA...

Individual 3. ...CGTAACGCTATTGCGC**CCTAGCTCTAGTGC**CATGCCGGATGA...

Individual 4. ...CGTAACGCTATTGCGC**CTAGCGAAGAAGT**CATGCCGGATGA...

Individual 5. ...CGTAACGCTATTGCGC**CTTACGATAAGCT**CATGCCGGATGA...

## Restriction fragment length polymorphism (RFLP)

However, in the past especially, use was often made of 'restriction endonuclease' enzymes that cut DNA at specific recognition sites situated along its length and so split an original strand of DNA into fragments. Individuals differ, as a result of largely neutral mutations, in the location of these sites, and so they differ, too, in the lengths of the fragments generated, these lengths being monitored by electrophoresis.

This variation, within a population, is known as restriction fragment length polymorphism, RFLP and there are therefore separate polymorphisms for different restriction enzymes (because their recognition sites differ). Samples can thus be subjected in turn to a series of enzymes, and the most differentiated individuals will then differ in the greatest number of RFLPs. Its disadvantage, of course, is that it utilizes only a small part of the underlying sequence variation.

### 8.2.1 Differentiation within species

albatrosses

Albatrosses, wide ranging sea birds with the largest wingspans of any birds alive today, have achieved iconic status by virtue of their appearance in poems and stories, but of the 21 species normally recognized, 19 are regarded as ‘threatened’ with extinction and the other two as ‘near threatened’. The black-browed albatross has recently been split by taxonomists into two species: *Thalassarche impavida*, found only on Campbell Island, between New Zealand and Antarctica, and *T. melanophris*, with breeding populations elsewhere in the sub-Antarctic, including the Falkland Islands, South Georgia and Chile (Figure 8.3a). The gray-headed albatross, *T. chrysostoma*, similar in size, also breeds on a number of sub-Antarctic islands, including South Georgia. The black-browed species usually remain associated with coastal shelf systems, whereas gray-headed albatrosses are far more ‘oceanic’ in their feeding grounds, but both, like all albatross species, are thought to return very close to their place of birth to breed (natal philopatry).



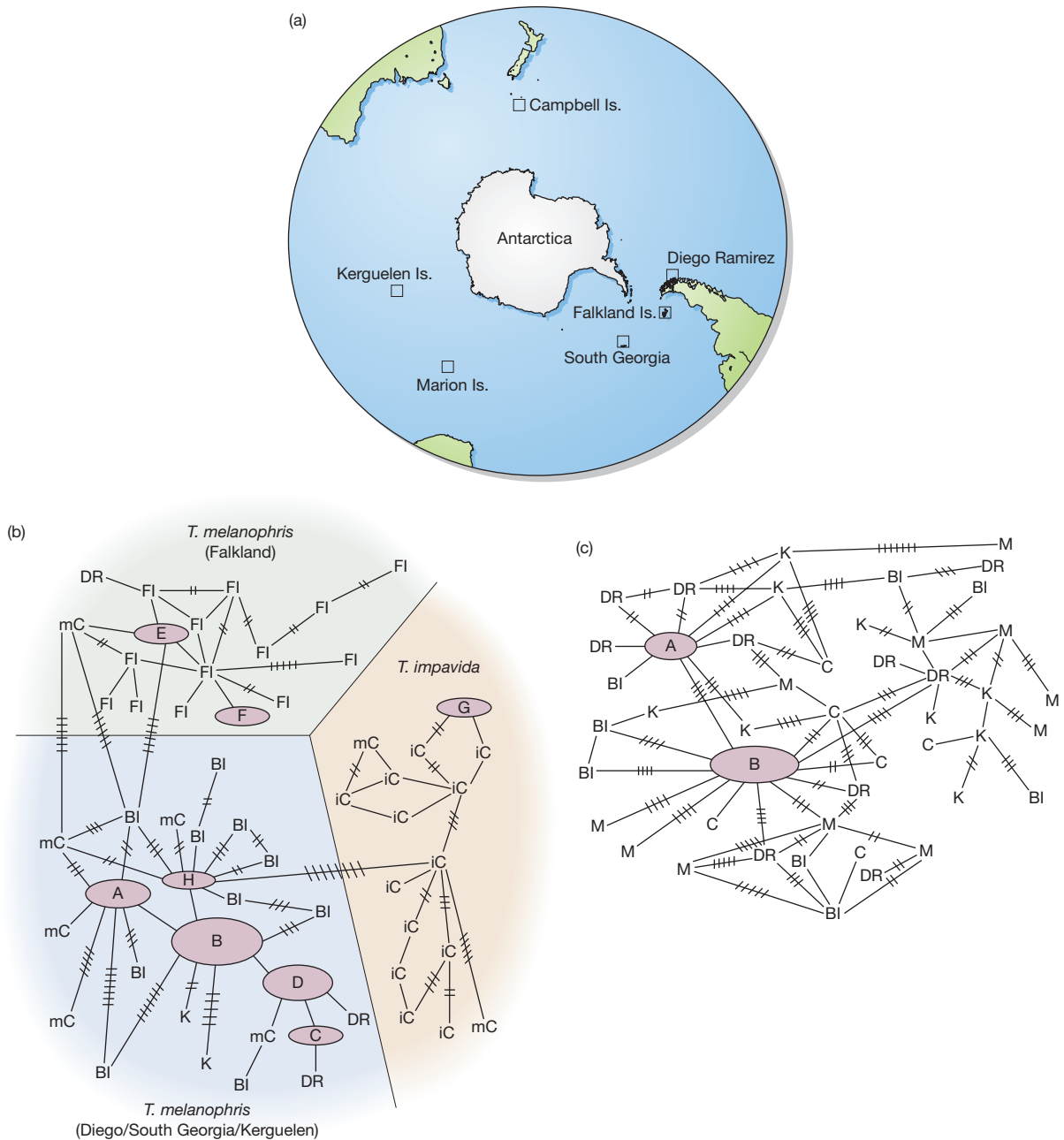


Figure 8.3

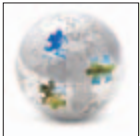
Population differentiation in albatrosses: black-browed albatrosses, *Thalassarche melanophris* and *T. impavida*, and the gray-headed albatross, *T. chrysostoma*. (a) Distribution of sites in the sub-Antarctic from which samples were taken. (b) The relationships amongst 73 black-browed albatrosses in the base sequence at a focal, variable site in their mtDNA. Where individuals from the same site shared exactly the same sequence, those individuals have been assigned a letter code (A, B, etc.) and placed in an oval proportional in size to the number of individuals. Individuals that do not fall into these groups, having a sequence unique within the data set, are identified as follows: BI, South Georgia, DR, Diego Ramirez (Chile), FI, Falkland Islands, K, Kerguelen Island (all *T. melanophris*); mC, *T. melanophris* from Campbell Island; and iC, *T. impavida* from Campbell Island. The cross-hatches represent the number of base differences between the individuals (or groups) they join. The samples fall into three 'clusters': *T. impavida*, *T. melanophris* from the Falkland Islands and *T. melanophris* from all other sites. Note though that the clustering is not perfect – as is normal, like the separation between the populations – and that some of the *T. melanophris* found on Campbell Island were identifiable as *T. melanophris*–*T. impavida* hybrids. (c) The relationships amongst 50 gray-headed albatrosses in the base sequence at a focal, variable site in their mtDNA. Coding is the same as in (b) except that M is Marion Island and C is Campbell Island. No separate clusters are discernable in this case.

With numbers in all sites declining year on year, therefore, the questions arise: 'How connected or separate are these populations? Should conservation efforts be directed at what are currently perceived to be whole species, or at particular breeding populations?'

These questions were addressed, in both species, by a study that used both mtDNA sequences and a panel of seven microsatellites (Burg & Croxall, 2001). The results were clearest for mtDNA (Figure 8.3b, c), but those for the microsatellites told the same story. For the black-browed species (Figure 8.3b), the molecular data confirmed the taxonomists' view that *T. impavida* was a separate species, but also demonstrated breeding between this species and *T. melanophris* on Campbell Island and indeed the production of hybrids between these two species there. More surprisingly, these data also demonstrated that the Falkland Islands support a breeding population of *T. melanophris* that is quite separate from an effectively indivisible population shared by Diego Ramirez (Chile), South Georgia and Kerguelen Island (in spite of the natal philopatry to these three sites). By contrast, the wider ranging gray-headed albatrosses, from all five of their sites, seemed to represent a single breeding population (Figure 8.3c) – again in spite of their natal philopatry.

From a conservation point of view, though, the most important conclusion relates to *T. melanophris*. Whereas previously the relative stability of the large Falkland Islands population was taken as insurance against a real vulnerability of the species to extinction, now, in the light of these molecular data, the Falkland Islands population should be considered as somewhat separate from the rest of the species, which itself is far more threatened with extinction than was previously appreciated. (A more active and immediate role for molecular markers in practical matters of conservation is described in Box 8.2.)

molecular markers in  
conservation



## 8.2 Topical ECOncerns

### The forensic analysis of the origins of our food

As we shall discuss more fully in Chapter 12, there is an increasingly frequent conflict between exploiting natural populations as a necessary source of food and conserving those same populations, both as an end in itself and so that future generations have something to eat. In Canada, for example, Pacific salmonid fish are harvested from a large number of commercial (industrial) and sport fisheries, each managed in its own way in an attempt to ensure its continued viability. So, for instance, a fishery may be closed altogether at times when fish from other sources are readily available, in order to allow the stock to breed and recover. Nonetheless, threats to

sustainability are very real: 2002 saw the first designation of a Canadian salmon stock, the Interior Fraser River coho salmon, as 'endangered', and many others require careful protection.

In an ideal world, policing, and hence management, of the different fisheries would be perfectly effective. But in reality, illegal fishing is bound to take place and cannot necessarily be countered simply by catching offenders 'in the act'. An alternative, then, or at least another weapon in the managers' armoury, is to be able to identify fish as having been illegally obtained at some other point in the chain from being caught to being eaten. Molecular markers make this possible.

**Table 8.1**

Species identification of salmonid samples obtained by fisheries officers in Canada because the material was believed to have been obtained illegally.

CASE (YEAR)	TISSUES	RESULT	LEGAL OUTCOME	FINE (\$)
1 (1995)	Blood/scales/slime from containers	Coho	Conviction	1500
2 (1998)	Muscle	Chum	Conviction	1800
		Chinook		
		Coho		
3 (1998)	Muscle	Coho	Conviction	?
4 (1999)	Muscle	Atlantic	No charges	—
		Chinook		
		Coho		
5 (2000)	Muscle	Coho	Guilty plea	7500
6 (2000)	Muscle	Sockeye	Conviction	1000

AFTER WITHER ET AL., 2004

**Table 8.2**

Stock identification of salmonid samples obtained by fisheries officers in Canada because the material was believed to have been obtained illegally. IF&T refers to the Interior Fraser and Thompson tributaries.

CASE (YEAR)	SPECIES	RESULTS	OUTCOME	FINE (\$)
1 (1998)	Sockeye	96.5% Fraser; 96.5% IF&T	Guilty plea	2,000
2 (1999)	Sockeye	100% Fraser; 100% IF&T	Conviction	15,000
3 (1999)	Chinook	91.4% Fraser	No conviction, under appeal	
4 (2000)	Sockeye	100% Fraser; 100% IF&T	Guilty plea	8,000
5 (2001)	Sockeye	97.8% Fraser; 97.8% IF&T	Guilty plea	3,000

AFTER WITHER ET AL., 2004

For example, the 10 species of Pacific salmon, *Oncorhynchus* spp., can be effectively distinguished from one another by RFLP profiling of targeted nuclear genes (Withler et al., 2004). Some results of applying such analyses to cases of suspected illegal possession of salmon are shown in Table 8.1. Case 2, for instance, involved a disaffected chef reporting a restaurant owner to the authorities. A fish was identified as a coho salmon, *O. kisutch*, which, because it showed no signs of having been frozen, could not have come from the previous years' legal harvest. The owner was duly fined.

Moreover, analyses based largely on micro-satellites, with their finer scale of resolution, are able, even within a species, to tie a sample to a particular river – if not with certainty then at least with a very high probability. Some results of these analyses are

shown in Table 8.2. In case 2 here, for instance, illegally sourced Fraser River sockeye salmon, *O. nerka*, were identified in an analysis of 50 cans of salmon and the defendant, fined \$15,000, was found to be in possession of 100,000 cans with a 'street value' of \$300,000–400,000.

*What do you think of the level of the fines imposed? How does the seriousness of crimes like this compare to those of other crimes: street robbery or the possession of illegal drugs for personal use? Should those convicted be punished in proportion to the economic harm they may be doing to these particular fisheries, or should their fines be seen as a signal sent out to all those who ignore the need to restrain activity in exploited but vulnerable populations and to conserve them for future generations?*

### 8.2.3 Differentiation between species: the red wolf

species or hybrid?

Issues in conservation surface again when we shift our focus from differentiation within to differentiation between species. The red wolf, *Canis rufus*, once had a widespread distribution in the southeastern United States (Figure 8.4a), but when, by the mid-1970s, that distribution had shrunk to a single population in eastern Texas, the US Fish and Wildlife Service instituted an emergency program to save it from extinction. Fourteen individuals were rescued from its final refuge and bred in captivity with a view to subsequent reintroduction in the wild. In the United States as a whole, the red wolf coexists with two other, closely related species, the gray wolf, *C. lupus*, and the coyote, *C. latrans*. Traditional analyses, based on morphological features, placed the red wolf as a genuine, separate species, intermediate in many ways between the gray wolf and the coyote (Nowak, 1979). However, as we shall see below, molecular markers suggest strongly that the red wolf is a hybrid arising from interbreeding between gray wolves and coyotes. A number of questions therefore suggest themselves (Wayne, 1996), including: ‘Should the conservation status of the red wolf, and the amount of money spent on its conservation, be downgraded if it is acknowledged that it is ‘only’ a hybrid and not a full species?’ And will attempts to save the red wolf by reintroduction be doomed, in any case, because of ‘introgression’ – the movement of genes from gray wolves or coyotes into the red wolf gene pool as a result of interbreeding?

mtDNA

The first molecular markers used to assess the degree of genetic isolation of red wolves from gray wolves and coyotes, albeit for a relatively small sample, were from mtDNA – both restriction fragment genotypes (RFLPs – see Box 8.1) and sequence variation within the cytochrome *b* gene. From the restriction site analysis carried out on contemporary captures (Figure 8.4b), it is clear, first, that the gray wolf and coyote samples were quite separate from one another; but also that samples from captive red wolves all fitted squarely within the cluster of coyote genotypes. And when sequence analysis was applied to museum pelts of red wolves from a variety of locations, and to a number of contemporary gray wolves and coyotes (Figure 8.4c), these too showed separate clusters for gray wolves and coyotes, and this time that red wolves had either gray wolf or coyote genotypes. Thus, the status of the red wolf as a separate species was called seriously into question, and its origin as a gray wolf–coyote hybrid was further supported by the observation of common, contemporary introgression of coyote genes into gray wolf populations throughout a region on the USA–Canadian border, where recent contact (the last 100 years) has been made as coyotes have moved north (Lehmann et al., 1991).

nuclear microsatellites

Investigations of microsatellites in the nuclear DNA have further clarified the red wolf story (Roy et al., 1994). First, studies on the USA–Canadian border confirmed the high frequency of contemporary coyote introgression into gray wolf gene pools (Figure 8.4d). Second, an analysis of 40 captive red wolves revealed that every one of the 53 microsatellite alleles they carried was also found in coyotes. Museum specimens of red wolves, too, failed to turn up unique red wolf alleles, and indeed, the historical and contemporary red wolf samples were themselves very similar. Finally, overall, red wolf samples, like contemporary gray wolf samples in the zone of hybridization, appear intermediate between coyotes and non-hybridizing gray wolves (Figure 8.4d). All of this argues in favor of the red wolf having its origins in gray wolf–coyote hybridization, with

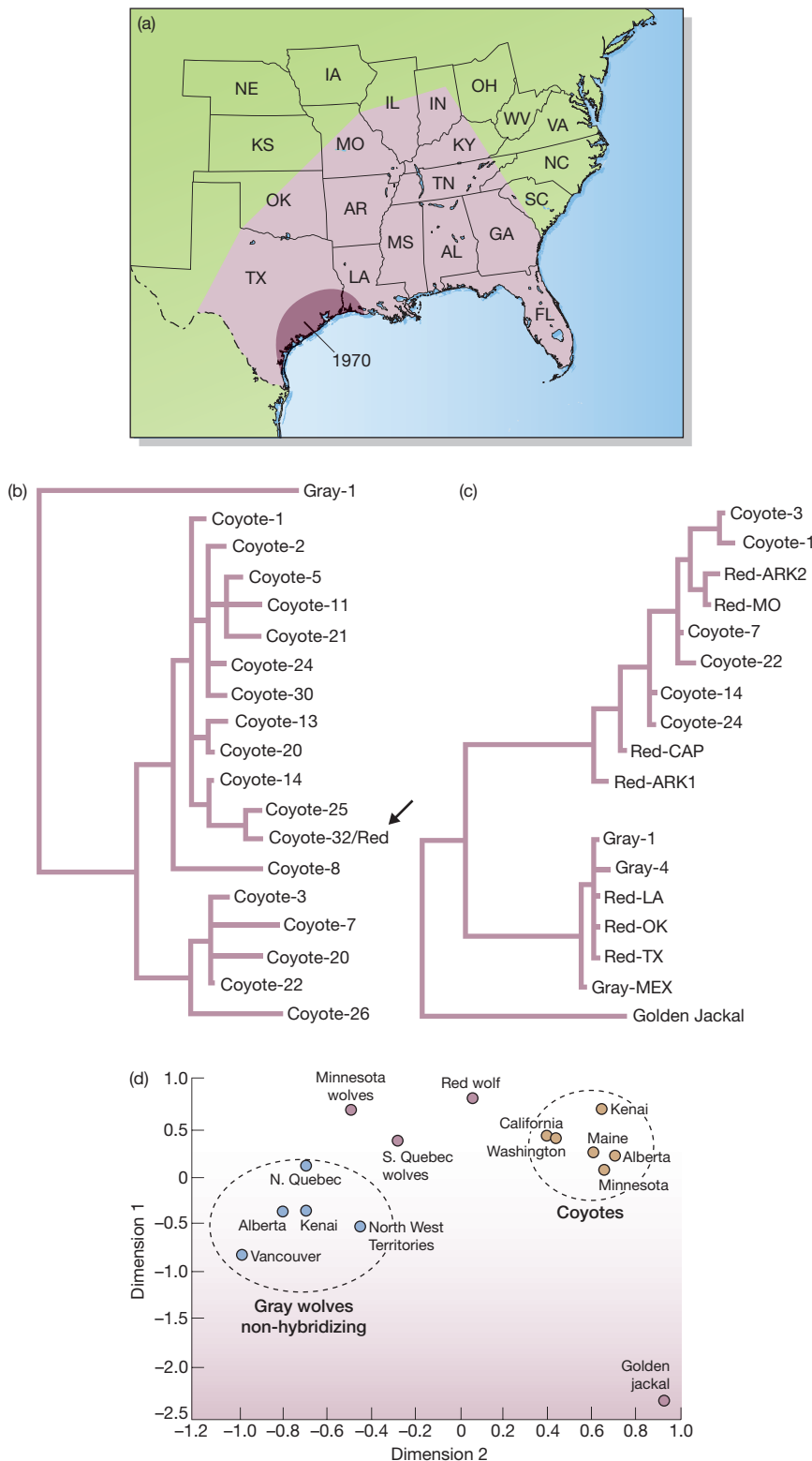


Figure 8.4

(a) The geographic range (light maroon) of the red wolf, *Canis rufus*, in the United States around 1700, and within that the smaller bounded area showing its range in southeastern Texas around 1970. (b) A 'phylogenetic tree' of coyote and red wolf mtDNA restriction-site genotypes (RFLPs). In a phylogenetic tree, the most similar (closely related) types are placed closest together, then linked to the type that is most similar to them, and so on, the lengths of the horizontal lines representing the degree of difference. The tree is 'rooted' (to give it context) by inclusion of a gray wolf (Gray-1). The numbers refer to different individuals. The arrow points to the single genotype shared by the eight captive red wolves that were sampled, which is clearly simply part of the coyote 'cluster'. (c) A phylogenetic tree constructed on similar principles but based on sequences of the cytochrome *b* gene in the mtDNA. Museum red wolf samples are from Arkansas (ARK), Missouri (MO), Louisiana (LA), Oklahoma (OK) and Texas (TX); CAP refers to a captive red wolf; and MEX refers to a gray wolf from Mexico. The tree is rooted by the inclusion of sequence data from the golden jackal, *C. aureus*. The red wolf genotypes are clearly parts of either the coyote or the gray wolf clusters. (d) The relationships between various coyote, gray wolf and red wolf populations at 10 nuclear DNA microsatellite loci, as demonstrated by an analysis that condenses the data from these 10 loci into two dimensions. The details of this analysis are unimportant here, as long as it is appreciated that the most similar populations are closest together in the figure. There are two clusters: coyotes and gray wolves from populations in which there is no hybridization with coyotes. Red wolves, and the populations of gray wolves from Minnesota and south Quebec where there is hybridization with coyotes, are located between these two clusters. Context, again, is provided by the location of the golden jackal.

subsequent further hybridization with coyotes, as gray wolves became rare in the southeastern USA.

In answer to our original questions, then, (i) the red wolf seems, ultimately, to be a hybrid rather than a separate species with a more ancient origin, and (ii) any program of reintroduction clearly is in danger of failing as a result of introgression from coyotes, requiring sufficient densities of red wolves to minimize this possibility, and perhaps even barriers to the ‘species’ meeting (Fredrickson & Hedrick, 2006). However, whether biological status and practical difficulties combine to undermine even the desirability of reintroducing red wolves is not simply a scientific question. Public perception and opinion (in this case regarding the conservation importance of the red wolf) must also be taken into account. Similar remarks apply to most conservation issues, especially when public funds are involved. A molecular ecology perspective has been immensely informative – but information may sometimes muddy rather than clarify the waters.

## 8.3 Coevolutionary arms races

We turn now from evolution at the molecular level to evolution at the level of species interactions, starting with those in which species are ‘in opposition’ to one another. Following some general background, we turn first to interactions between insects and the plants they eat (Section 8.3.2) and then to those between parasites and their hosts (Section 8.3.3).

### 8.3.1 Coevolution

The dynamics of consumer resource pairs (see Chapter 7) are linked to the dynamics of whole webs of interacting species (see Chapter 9) by how specialized or generalized particular consumers are. Generalists draw the species of a community together into large interactive networks. Specialists divide communities into detached or semidetached compartments. Coevolution plays a vital part in determining how specialized or generalized particular consumers are.

It is not surprising, as we saw in Chapter 3, that many organisms have evolved defenses that reduce the chance of an encounter with a consumer and/or increase the chance of surviving such an encounter. But the interaction does not necessarily stop there. A better defended food resource (the ‘prey’) itself exerts a selection pressure on consumers to overcome that defense. A consumer that does so is likely to have invested in counteracting that defense as opposed to others, and will steal a march on its competitors, and so is likely to become relatively specialized on that prey type – which is then under particular pressure to defend itself against that particular consumer, and so on. A continuing interaction can therefore be envisaged in which the evolution of both the consumer and the prey depend crucially on the evolution of the other: what Ehrlich and Raven (1964) called a coevolutionary ‘arms race’, which, in its most extreme form, has a coadapted pair of species locked together in perpetual struggle.

Indeed, what is unacceptable to most animals may be the chosen, even unique, diet of others. It is, after all, an inevitable consequence of having evolved resistance to a prey’s defenses that a consumer will have gained access to a resource unavailable to most (or all) other species. For example, the tropical legume *Dioclea metacarpa*

one man’s poison is another  
man’s meat



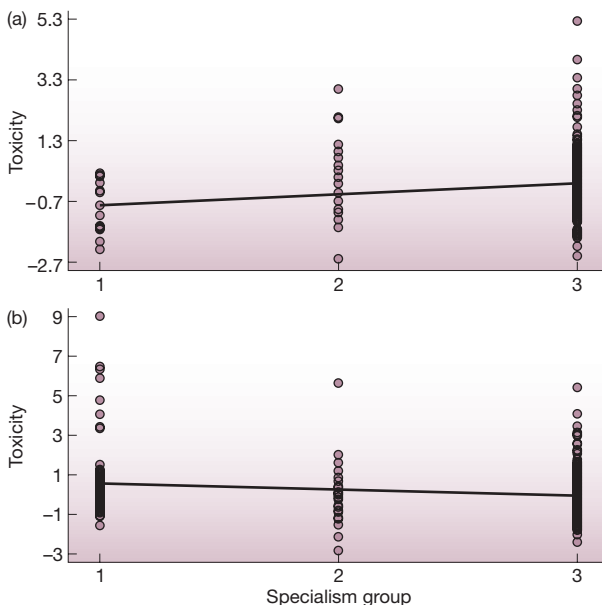
is toxic to almost all insect species because it contains a non-protein amino acid, L-canavanine, which those insects incorporate (lethally) into their proteins in place of arginine. But a species of bruchid beetle, *Caryedes brasiliensis*, has evolved a modified enzyme that distinguishes between L-canavanine and arginine, and the larvae of these beetles feed solely on *D. metacarpa* (Rosenthal et al., 1976).

### 8.3.2 Insect–plant arms races

We discussed in Section 3.4.2 how attacks by herbivores select for plant-defensive chemicals. We also saw that these can be divided into ‘qualitative’ chemicals that are poisonous, can kill in small doses and tend to be induced by herbivore attacks, and ‘quantitative’ chemicals that are digestion-reducing, rely on an accumulation of ill effects and tend to be produced constitutively (i.e. all the time). These chemicals will select for adaptations in herbivores that can overcome them. It seems probable, however, that toxic chemicals, by virtue of their specificity, are likely to be the foundation of an arms race, requiring an equally specific response from a herbivore; whereas chemicals that make plants generally indigestible are much more difficult to overcome through any ‘targeted’ adaptation (Cornell & Hawkins, 2003). Put simply: plants relying on toxins are more prone to becoming involved in arms races with their herbivores (like the beetle and legume described above) than those relying on more ‘quantitative’ chemicals.

We can seek evidence for the toxin arms race hypothesis by asking whether specialist herbivores generally, locked in their coevolutionary arms races, perform better when faced with their plants’ toxic chemicals than generalists; whereas generalists, having invested in overcoming a wide range of chemicals, perform better than specialists when faced with chemicals that have not provoked coevolutionary responses. Such evidence is provided by an analysis of a wide range of data sets for insect herbivores fed on artificial diets with added chemicals (892 insect–chemical combinations; Figure 8.5).

specialists are more prone to arms races



**Figure 8.5**

Combining data from a wide range of published studies, insect herbivores were split into three groups: 1, specialists (feeding from one or two plant families); 2, ‘oligophages’ (3–9 families); and 3, generalists (more than nine families). Chemicals were split into two groups: (a) those that are found in the normal hosts of the specialists and oligophages, and (b) those that are not. ‘Toxicity’ is measured from the mortality rates of insects on a standardized scale, since many studies have been combined. (a) It is apparent that more specialized insects suffered lower mortality on chemicals that have provoked a coevolutionary response from specialist herbivores. (b) It is apparent that more generalist insects suffered lower mortality on chemicals that have *not* provoked a coevolutionary response from specialist herbivores.  $P < 0.005$  in both cases.

### 8.3.3 Coevolution of parasites and their hosts

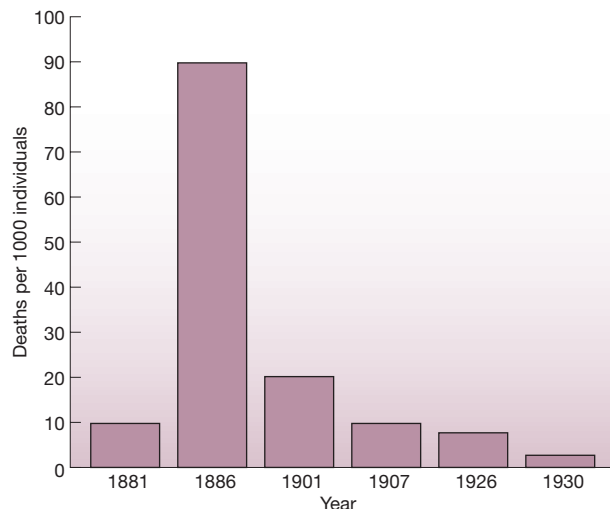
The intimate association between parasites and their hosts makes them especially prone to coevolutionary arms races. Indeed, the specialization may go further than that between species. Within species, it is common to find a high degree of genetic variation in the virulence of parasites and/or in the resistance or immunity of hosts. Every few years, for example, as we are perhaps more aware than ever, a new strain of the influenza virus evolves of sufficient virulence and novelty to generate a widespread epidemic and mortality in human populations that had been relatively resistant to previously circulating strains. No strain has been more devastating – at the time of writing – than the worldwide epidemic (*pandemic*) of Spanish flu that followed World War I in 1918/19 and killed 20 million people – many more than died in the war itself. Human diseases can also provide examples of variation in host resistance. When the Native Americans of the Canadian Plains were forcibly settled onto reservations in the 1880s, their death rate due to tuberculosis (TB) initially exploded but then gradually declined (Figure 8.6). Environmental factors (inadequate diet, overcrowding, spiritual demoralization) undoubtedly played some part in this, but variation in resistance is also likely to have been significant. The mortality rate among the Native Americans was often 20 times that of the surrounding European colonist population, living in similar conditions but having been exposed previously to TB. Some native families had a particularly low mortality rate in the 1880s epidemic, and many of the survivors in the 1930s were descendants of those families (Ferguson, 1933; Dobson & Carper, 1996).

myxomatosis

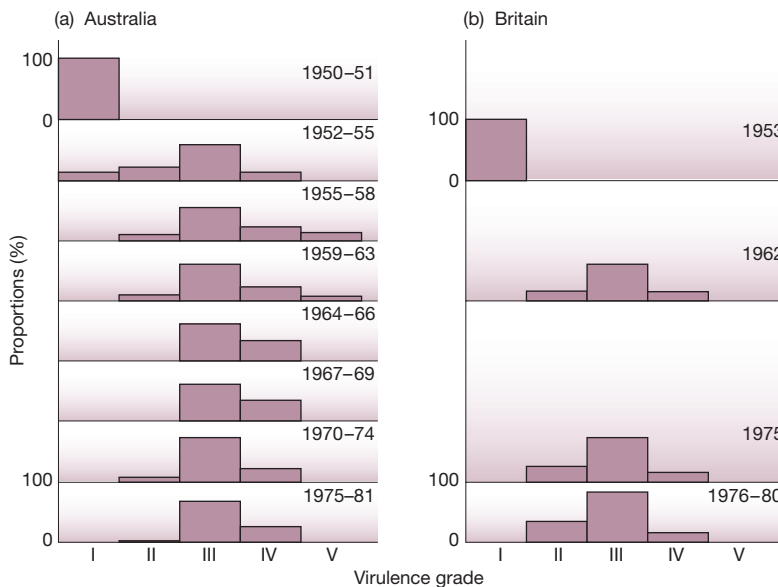
It may seem straightforward that parasites in a population select for the evolution of more resistant hosts, which in turn select for more infective parasites: a classic arms race. In fact, the process is not necessarily so straightforward, though there are certainly examples where host and parasite drive one another's evolution. A most dramatic example involves the rabbit and the myxoma virus, which causes myxomatosis. The virus originated in the South American jungle rabbit *Sylvilagus brasiliensis*, where it causes a mild disease that only rarely kills

**Figure 8.6**

The mortality rate due to tuberculosis in three generations of Canadian Plains Native Americans after their forced settlement onto reservations.



AFTER FERGUSON, 1933; DOBSON & CARPER, 1996

**Figure 8.7**

(a) The percentages in which various grades of myxoma virus have been found in wild populations of rabbits in Australia at different times from 1951 to 1981. Grade I is the most virulent. (After Fenner, 1983.) (b) Similar data for wild populations of rabbits in Great Britain from 1953 to 1980.

the host. The South American virus, however, is usually fatal when it infects the European rabbit *Oryctolagus cuniculus*. In one of the greatest examples of biological pest control, the myxoma virus was introduced into Australia in the 1950s to control the European rabbit, which had become a pest of grazing lands. The disease spread rapidly in 1950/51, and rabbit populations were greatly reduced – by more than 90% in some places. At the same time, the virus was introduced to England and France, and there too it resulted in huge reductions in the rabbit populations. The evolutionary changes that then occurred in Australia were followed in detail by Fenner and his associates, who had the brilliant foresight to establish baseline genetic strains of both rabbits and virus (Fenner, 1983). They used these to measure subsequent changes in the virulence of the virus and the resistance of the host as they evolved in the field.

When the disease was first introduced to Australia it killed more than 99% of infected rabbits. This ‘case mortality’ fell to 90% within 1 year and then declined further. The virulence of virus isolates was graded according to host survival time and the case mortality of control rabbits. The original, highly virulent virus was grade I, which killed > 99% of infected laboratory rabbits. Already by 1952, most of the virus isolates from the field were the less virulent grades III and IV. At the same time, the rabbit population in the field was increasing in resistance. When injected with a standard grade III strain, field samples of rabbits in 1950/51 had a case mortality of nearly 90%, which had declined to less than 30% only 8 years later (Figure 8.7).

This evolution of resistance is easy to understand: resistant rabbits are obviously favored by natural selection in the presence of the myxoma virus. The case of the virus, however, is subtler. The contrast between the virulence of the virus in the European rabbit and its lack of virulence in the American host with which it had coevolved, combined with the attenuation of its virulence in Australia and Europe after its introduction, fit a commonly held view that parasites evolve toward

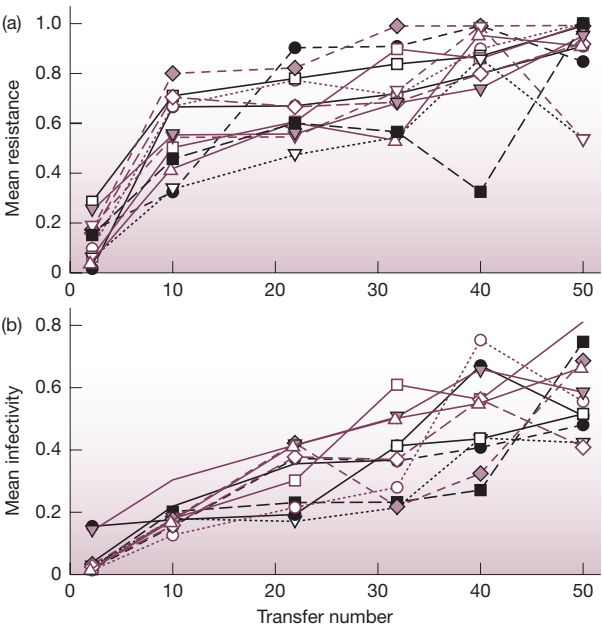
becoming benign to their hosts in order to prevent the parasite eliminating its host and thus eliminating its habitat. This view, however, is quite wrong. The parasites favored by natural selection are those with the greatest fitness (broadly, the greatest reproductive rate). Sometimes this is achieved through a decline in virulence, but sometimes it is not. In the myxoma virus, an initial decline in virulence was indeed favored – but further declines were not.

The myxoma virus is blood-borne and is transmitted from host to host by blood-feeding insect vectors. In the first 20 years after its introduction to Australia, the main vectors were mosquitoes, which feed only on live hosts. The problem for grade I and II viruses is that they kill the host so quickly that there is only a very short time in which the mosquito can transmit them. Effective transmission may be possible at very high host densities, but as soon as densities decline, it is not. Hence, there was selection against grades I and II and in favor of less virulent grades, giving rise to longer periods of host infectiousness. At the other end of the virulence scale, however, the mosquitoes are unlikely to transmit grade V of the virus because it produces very few infective particles. The situation was complicated in the late 1960s when an alternative vector of the disease, the rabbit flea *Spilopsyllus cuniculi* (the main vector in England), was introduced to Australia, apparently favoring more virulent strains than the mosquitoes had done. Overall, however, there has been selection in the rabbit–myxomatosis system not for decreased virulence as such, but for *increased transmissibility* (and hence increased fitness) – which happens in this system to be maximized at intermediate grades of virulence.

#### bacteria and bacteriophage

In other cases, host–parasite coevolution is more definitely antagonistic: increased resistance in the host and increased infectivity in the parasite. A classic example is the interaction between agricultural plants and their pathogens (Burdon, 1987), though in this case the resistant hosts are often introduced by human intervention. There may even be gene-for-gene matching, with a particular virulence allele in the pathogen selecting for a resistant allele in the host, which in turn selects for alleles other than the original allele in the pathogen, and so on. In fact, these detailed processes have proved difficult to observe, but this has been done with a system comprising the bacterium *Pseudomonas fluorescens* and its viral parasite, the bacteriophage (or phage) SBW25 $\phi$ 2, where such evolution is relatively easy to observe because generation times are so short. Changes in both host and parasite were monitored as 12 replicate coexisting populations of bacterium and phage were transferred from culture bottle to culture bottle. It is apparent that the bacteria became generally more resistant to the phage at the same time as the phage became generally more infective to the bacteria: each was being driven by the directional selection of an arms race (Figure 8.8).

This was only apparent, however, because each bacterial strain (from one of the 12 replicate pairs) was tested against all 12 phage strains, and each phage strain tested against all bacterial strains, and mean resistances and infectivities calculated. When, at the end of the experiment (Table 8.3), the resistance of each bacterial strain was tested against each phage strain in turn, it was clear that bacteria were almost always *most* resistant (and often wholly resistant) to the phage strain with which they coevolved. Clearly, the specific problems posed by particular phage strains had provoked equally specific evolutionary responses on the part of the bacterial strains.



**Figure 8.8**  
(a) Over evolutionary time (1 'transfer'  $\approx$  8 bacterial generations) bacterial resistance to phage increased in each of 12 bacterial replicates (designated by different symbols). 'Mean' resistance was the mean calculated over the 12 phage isolates from the respective time points. (b) Similarly, phage infectivity increased, where 'mean' infectivity was calculated over the twelve bacterial replicates.

**Table 8.3**

For each of 12 bacterial replicates (B1–B12) and their 12 respective phage replicates ( $\phi$ 1– $\phi$ 12), entries in the table are the proportion of bacteria resistant to the phage at the end of a period of coevolution (50 transfers  $\approx$  400 bacterial generations). Coevolving pairs are shown along the diagonal in bold. Note that bacterial strains are usually most resistant to the phage strain with which they coevolved.

PHAGE REPLICATES	BACTERIAL REPLICATES											
	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12
$\phi$ 1	<b>0.8</b>	0.9	1	1	1	1	1	1	0.85	0.85	0.75	0.65
$\phi$ 2	0.1	<b>1</b>	0.3	1	0.85	0.25	1	1	0.85	0.9	0.8	0.65
$\phi$ 3	0.75	0.75	<b>1</b>	1	1	0.9	1	1	0.85	0.9	0.9	0.65
$\phi$ 4	0.15	0.9	0.8	<b>1</b>	0.85	0.6	0.6	1	0.85	1	0.85	0.35
$\phi$ 5	0.25	0.9	1	1	<b>1</b>	0.9	1	0.8	0.85	1	0.8	0.65
$\phi$ 6	0.2	1	0.85	0.8	0.75	<b>0.8</b>	0.85	0.9	0.85	0.75	0.45	0.25
$\phi$ 7	0.2	0.75	0.6	1	0.4	0.45	<b>1</b>	0.9	0.85	1	0.75	0.35
$\phi$ 8	0	0.95	0.55	0.95	0.35	0.25	0.8	<b>1</b>	0.85	1	0.7	0.25
$\phi$ 9	0	0.7	0.55	0.45	0.7	0.35	1	1	<b>0.85</b>	1	0.5	0.1
$\phi$ 10	0	0.7	0.9	0.7	0.55	0.9	1	1	0.7	<b>1</b>	0.5	0.4
$\phi$ 11	0	0.5	0.9	0.75	0.7	1	1	0.95	0.75	1	<b>1</b>	0.35
$\phi$ 12	0	0.15	0	0.1	0.65	0.35	1	1	0.7	0.8	0.85	<b>0.4</b>

## 8.4 Mutualistic interactions

No species lives in isolation, but often the association with other species is especially close: for many organisms, the habitat they occupy is an individual of another species. Parasites live within the body cavities or even the cells of their hosts, nitrogen-fixing bacteria live in nodules on the roots of leguminous plants,

symbiosis and mutualism

and so on. *Symbiosis* ('living together') is the term that has been coined for such close physical associations between species, in which a 'symbiont' occupies a habitat provided by a 'host'. In fact, though, parasites are usually excluded from the category of symbionts, which is reserved instead for interactions where there is at least the suggestion of *mutualism*. A mutualistic relationship is simply one in which organisms of different species interact to their mutual benefit. Mutualism, therefore, need not involve close physical association: mutualists need not be symbionts. For example, many plants gain dispersal of their seeds by offering a reward to birds or mammals in the form of edible fleshy fruits, and many plants assure effective pollination by offering a resource of nectar in their flowers to visiting insects. These are mutualistic interactions but they are not symbioses.

mutualism: reciprocal exploitation  
not a cosy partnership

It would be wrong, however, to see mutualistic interactions simply as conflict-free relationships from which nothing but good things flow for both partners. Rather, current evolutionary thinking views mutualisms as cases of reciprocal exploitation where nonetheless each partner is a *net* beneficiary (Herre & West, 1997).

Mutualisms themselves have often been neglected in the past compared to other types of interaction, yet mutualists compose most of the world's biomass. Almost all the plants that dominate grasslands, heaths and forests have roots that have an intimate mutualistic association with fungi. Most corals depend on the unicellular algae within their cells, many flowering plants need their insect pollinators, and many animals carry communities of microorganisms within their guts that they require for effective digestion.

The rest of this section is organized as a progression. We start with mutualisms in which no intimate symbiosis is involved; rather, the association is largely behavioral: that is, each partner behaves in a manner that confers a net benefit on the other. By Section 8.4.4, when we discuss mutualisms between animals and the microbiota living in their guts, we will have moved on to closer associations (one partner living within the other), and in Sections 8.4.5 and 8.4.6 we examine still more intimate symbioses in which one partner enters between or within another's cells.

### 8.4.1 Mutualistic protectors

cleaner and client fish

'Cleaner' fish, of which at least 45 species have been recognized, feed on ectoparasites, bacteria and necrotic tissue from the body surface of 'client' fish. Indeed, the cleaners often hold territories with 'cleaning stations' that their clients visit – and visit more often when they carry many parasites. The cleaners gain a food source and the clients are protected from infection. In fact, it has not always proved easy to establish that clients benefit, but experiments off Lizard Island on Australia's Great Barrier Reef were able to do this for the cleaner fish, *Labroides dimidiatus*, which eats parasitic gnathiid isopods from its client fish, *Hemigymnus melapterus*. Clients had significantly (3.8 times) more parasites 12 days after cleaners were excluded from caged enclosures (Figure 8.9a); but even in the short term (up to 1 day), although removing cleaners, which only feed during daylight, had no effect when a check was made at dawn (Figure 8.9b), this led to there being significantly (4.5 times) more parasites following a further day's feeding (Figure 8.9c).

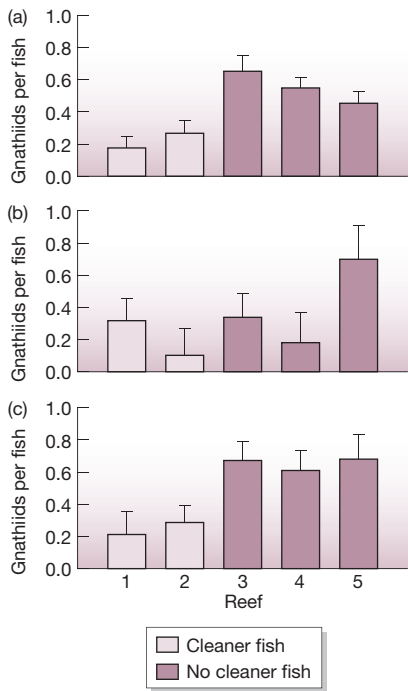


Figure 8.9

Cleaner fish really do clean their clients. The mean number of gnathiid parasites per client, *Hemigymnus melapterus*, at five reefs, from three of which cleaners, *Labroides dimidiatus*, were experimentally removed. (a) In a long-term experiment, clients without cleaners had more parasites after 12 days ( $F = 17.6$ ,  $P = 0.02$ ). (b) In a short-term experiment, clients without cleaners did not have significantly more parasites at dawn after 12 hours ( $F = 1.8$ ,  $P = 0.21$ ), presumably because cleaners do not feed at night. (c) However, the difference was significant after a further 12 hours of daylight ( $F = 11.6$ ,  $P = 0.04$ ). Bars are standard errors.

The idea that there are mutualistic, ‘protective’ relationships between plants and ants was put forward by Belt (1874) after observing the behavior of aggressive ants on species of *Acacia* with swollen thorns in Central America. For example, the Bull’s horn acacia (*Acacia cornigera*) bears hollow thorns that are used by its associated ant, *Pseudomyrmex ferruginea*, as nesting sites (Figure 8.10b); its

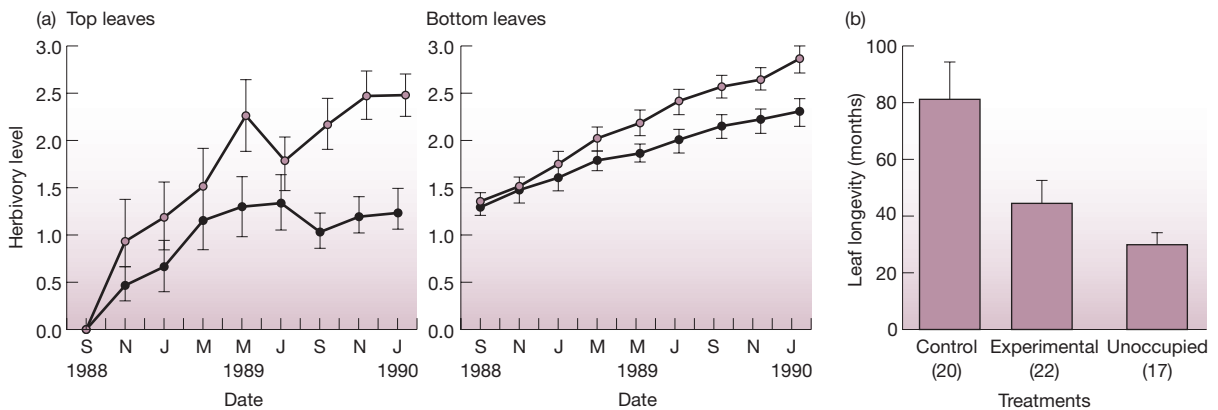
ant–plant mutualisms . . .



Figure 8.10

Structures of the Bull’s horn acacia (*Acacia cornigera*) that attract its ant mutualist. (a) Protein-rich Beltian bodies at the tips of the leaflets. (b) Hollow thorns used by the ants as nesting sites.





**Figure 8.11**

(a) The intensity of leaf herbivory (based on the cumulative proportion of leaf area removed) on plants of *Tachigali myrmecophila* naturally occupied by the ant *Pseudomyrmex concolor* (●,  $n = 22$ ) and on plants from which the ants had been experimentally removed (○,  $n = 23$ ). Bottom leaves were those present at the start of the experiment and top leaves were those emerging subsequently. (b) The longevity of leaves on plants of *T. myrmecophila* occupied by *P. concolor* (control) and from which ants were experimentally removed or from which ants were naturally absent. Error bars  $\pm$  SE.

... but do the plants benefit?

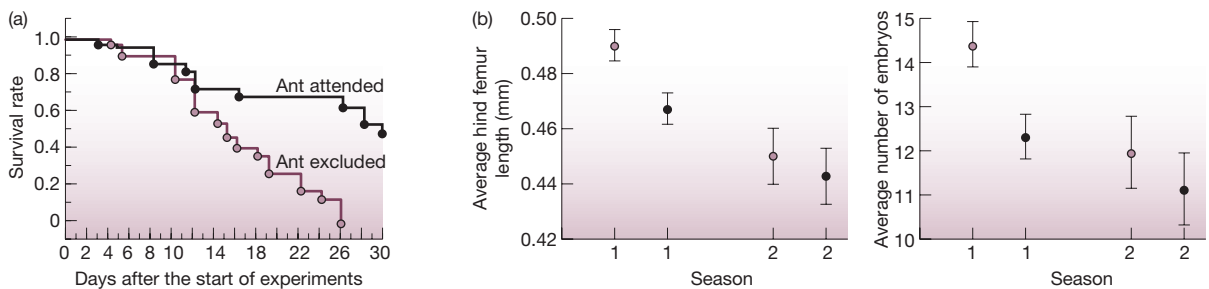
leaves have protein-rich 'Beltian bodies' at their tips (Figure 8.10a) which the ants collect and use for food; and it has sugar-secreting nectaries on its vegetative parts that also attract the ants. The ants, for their part, protect these small trees from competitors by actively snipping off shoots of other species and also protect the plant from herbivores – even large (vertebrate) herbivores may be deterred.

In fact, ant–plant mutualisms appear to have evolved many times (even repeatedly in the same family of plants); and nectaries are present on the vegetative parts of plants of at least 39 families and in many communities throughout the world. Their precise role is not easy to establish. They clearly attract ants, sometimes in vast numbers, but carefully designed and controlled experiments are necessary to show that the plants themselves benefit, such as a study of the Amazonian canopy tree *Tachigali myrmecophila*, which harbors the stinging ant *Pseudomyrmex concolor* in specialized hollowed-out structures (Figure 8.11). The ants were removed from selected plants. These then bore 4.3 times as many phytophagous insects as control plants and suffered much greater herbivory, such that leaves on plants that carried a population of ants lived more than twice as long as those on unoccupied plants and nearly 1.8 times as long as those on plants from which ants had been deliberately removed.

### 8.4.2 The culture of crops or livestock

human agriculture

At least in terms of geographic extent, some of the most dramatic mutualisms are those of human agriculture. The numbers of individual plants of wheat, barley, oats, corn and rice, and the areas these crops occupy, vastly exceed what would have been present if they had not been brought into cultivation. The increase in the human population since the time of hunter–gatherers is some measure of the reciprocal advantage to *Homo sapiens*. Even without doing the experiment, we can easily imagine the effect the extinction of humans would have on the world population of rice plants or the effect of the extinction of rice plants on the



**Figure 8.12**

(a) Ant-excluded colonies of the aphid *Tuberculatus quercicola* were more likely to become extinct than those attended by ants ( $\chi^2 = 15.9$ ,  $P < 0.0001$ ). (b) But in the absence of predators (experimentally removed), ant-excluded colonies performed better than those attended by ants. Shown are averages for aphid body size (hind femur length;  $F = 6.75$ ,  $P = 0.013$ ) and numbers of embryos ( $F = 7.25$ ,  $P = 0.010$ ),  $\pm$  SE, for two seasons (1: July 23 to August 11, 1998; 2: August 12 to August 31, 1998). Maroon circles, predator-free and ant-excluded treatment; black circles, predator-free and ant-attended treatment.

population of humans. Similar comments apply to the domestication of cattle, sheep and other mammals.

Similar ‘farming’ mutualisms have developed in termite and especially ant societies, where the farmers may protect individuals they exploit from competitors and predators and may even move or tend them. Ants, for example, farm many species of aphids (homopterans) in return for sugar-rich secretions of honeydew. The ‘flocks’ of aphids benefit through suffering lower mortality rates caused by predators, showing increased feeding and excretion rates, and forming larger colonies; but it would be wrong to imagine that this is a cosy relationship with nothing but benefits on both sides: the aphids are being manipulated – is there a cost to be entered on the other side of the balance sheet? This question has been addressed for colonies of the aphid *Tuberculatus quercicola* attended by the red wood ant *Formica yessensis* on the island of Hokkaido, northern Japan (Figure 8.12). As expected, in the presence of predators, aphid colonies survived significantly longer when attended by ants than when ants were excluded by smearing ant repellent at the base of the oak trees on which the aphids lived (Figure 8.12a). However, there *were* also costs for the aphids: in an environment from which predators were excluded, and the effects of ant attendance on aphids could thus be viewed in isolation, ant-attended aphids grew less well and were less fecund than those where ants as well as predators were excluded (Figure 8.12b).

aphids farmed by ants:  
do they pay a price?

### 8.4.3 The dispersal of seeds and pollen

Very many plant species use animals to disperse their seeds and pollen. About 10% of all flowering plants possess seeds or fruits that bear hooks, barbs or glues that become attached to the hairs, bristles or feathers of any animal that comes into contact with them. They are frequently an irritation to the animal, which often cleans itself and removes them if it can, but usually after carrying them some distance. In these cases the benefit is to the plant (which has invested resources in attachment mechanisms) and there is no reward to the animal.

Quite different are the true mutualisms between higher plants and the birds and other animals that feed on fleshy fruits and disperse the seeds. Of course, for the relationship to be mutualistic, it is essential that the animal digests only

seed dispersal

fruits

## pollination

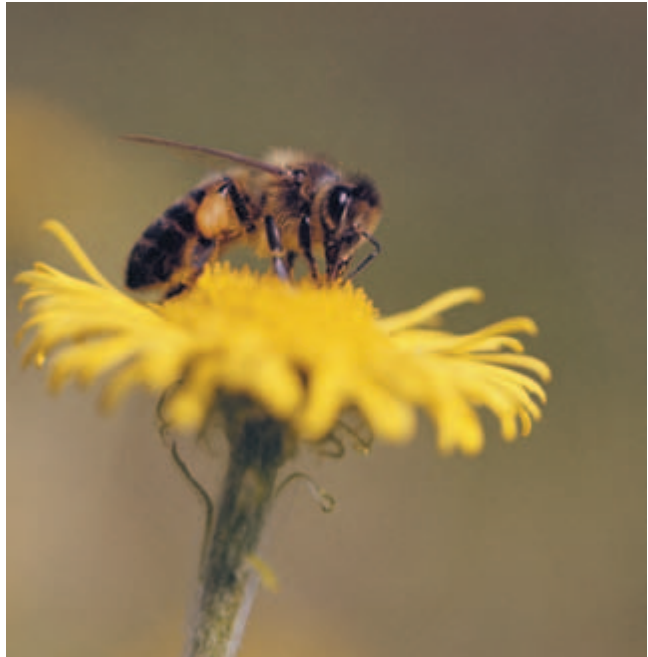
the fleshy fruit and not the seeds, which must remain viable when regurgitated or defecated. Thick strong defenses that protect plant embryos are usually part of the price paid by the plant for dispersal by fruit-eaters.

Many different kinds of animals have entered into pollination liaisons with flowering plants, including humming-birds, bats and even small rodents and marsupials (Figure 8.13). Most animal-pollinated flowers offer nectar, pollen or

**Figure 8.13**

Pollinators. (a) Honeybee (*Apis mellifera*) on raspberry flowers. (b) Cape sugarbird (*Promerops cafer*) feeding on *Protea eximia*.

(a)



(b)



both as a reward to their visitors. Floral nectar seems to have no value to the plant other than as an attractant to animals and it has a cost to the plant, because the nectar carbohydrates might have been used in growth or some other activity. Presumably, the evolution of specialized flowers and the involvement of animal pollinators have been favored because an animal may be able to recognize and discriminate between different flowers and so move pollen between different flowers of the same species but not to flowers of other species. Passive transfer of pollen, for example by wind or water, does not discriminate in this way and is therefore much more wasteful. On the other hand, where the vectors and flowers are highly specialized, as is the case in many orchids, virtually no pollen is wasted even on the flowers of other species.

The pollinators par excellence are, without doubt, the insects. Pollen is a nutritionally-rich food resource and in the simplest insect-pollinated flowers, pollen is offered in abundance and freely exposed to all and sundry. The plants rely for pollination on the insects being less than wholly efficient in their pollen consumption, carrying their spilt food with them from plant to plant. In more complex flowers, nectar (a solution of sugars) is produced as an additional or alternative reward. In the simplest of these, the nectaries are unprotected, but, with increasing specialization, nectaries are enclosed in structures that restrict access to the nectar to just a few visitor species. This range can be seen within the family Ranunculaceae. In the simple flower of *Ranunculus ficaria* the nectaries are exposed to all visitors, but in the more specialized flower of *R. bulbosus* there is a flap over the nectary, and in *Aquilegia* the nectaries have developed into long tubes and only visitors with long probosces (tongues) can reach the nectar. Unprotected nectaries have the advantage of a ready supply of pollinators, but because these pollinators are unspecialized they transfer much of the pollen to the flowers of other species. Protected nectaries have the advantage of efficient transfer of pollen by specialists to other flowers of the same species, but are reliant on there being sufficient numbers of these specialists.

Charles Darwin (1859) recognized that a long nectary, as in *Aquilegia*, forced a pollinating insect into close contact with the pollen at the nectary's mouth. Natural selection may then favor even longer nectaries, and as an evolutionary reaction, the tongues of the pollinator would be selected for increasing length: reciprocal coevolution. Nilsson (1988) deliberately shortened the nectary tubes of the long-tubed orchid *Platanthera* and showed that the flowers then produced many fewer seeds – presumably because the pollinator was not forced into a position that maximized the efficiency of pollination.

insect pollinators: from generalists to ultraspecialists

#### 8.4.4 Mutualistic gut inhabitants

Most of the mutualisms discussed so far have depended on patterns of behavior, where neither species lives entirely 'within' its partner. In many other mutualisms, one of the partners is a unicellular eukaryote or bacterium that is integrated more or less permanently into the body cavity or even the cells of its multicellular partner. The microbiota occupying parts of various animals' alimentary canals are the best known extracellular symbionts.

The crucial role of microbes in the digestion of cellulose by vertebrate herbivores has long been appreciated, but it now appears that the gastrointestinal tracts of all vertebrates are populated by a mutualistic microbiota. Protozoa and fungi are

the vertebrate gut

usually present but the major contributors to these ‘fermentation’ processes are bacteria. Their diversity is greatest in regions of the gut where the pH is relatively neutral and food retention times relatively long. In small mammals (e.g. rodents, rabbits, hares), the cecum is the main fermentation chamber, whereas in larger non-ruminant mammals such as horses the colon is the main site. In ruminants, like cattle and sheep, and in kangaroos and other marsupials, fermentation occurs in specialized stomachs (see Figure 3.24).

The basis of the mutualism is straightforward. The microbes receive a steady flow of substrates for growth in the form of food that has been eaten, chewed and partly homogenized. They live within a chamber in which the pH and, in endotherms, temperature are regulated and anaerobic conditions are maintained. The vertebrate hosts, especially the herbivores, receive nutrition from food that they would otherwise find, literally, indigestible. The bacteria produce short-chain fatty acids (SCFAs) by fermentation of the host’s dietary cellulose and starches and of the endogenous carbohydrates contained in host mucus and sloughed epithelial cells. SCFAs are often a major source of energy for the host: for example, they provide more than 60% of the maintenance energy requirements for cattle and 29–79% of those for sheep (Stevens & Hume, 1998). The microbes also convert nitrogenous compounds (amino acids that escape absorption in the midgut, urea that would otherwise be excreted by the host, mucus and sloughed cells) into ammonia and microbial protein, conserving nitrogen and water; and they synthesize B vitamins. The microbial protein is useful to the host if it can be digested – in the intestine by foregut fermenters and following coprophagy (eating their own feces) in hindgut fermenters – but ammonia is usually not useful and may even be toxic to the host.

### 8.4.5 Mycorrhizas

Most higher plants do not have roots, they have *mycorrhizas* – intimate mutualisms between fungi and root tissue. Plants of only a few families, such as the Cruciferae, are exceptions. Broadly, the fungal networks in mycorrhizas capture nutrients from the soil, which they transport to the plants in exchange for carbon. Many plant species can live without their mycorrhizal fungi in soils where neither nutrients nor water are ever limiting, but in the harsh world of natural plant communities, the symbioses, if not strictly obligate, are nonetheless ‘ecologically obligate’: that is, necessary if the individuals are to survive in nature (Buscot et al., 2000).

Generally, three major types of mycorrhiza are recognized. Arbuscular mycorrhizas are found in about two-thirds of all plant species, including most non-woody species and tropical trees. Ectomycorrhizal fungi form symbioses with many trees and shrubs, dominating boreal and temperate forests and also some tropical rain forests. Finally, ericoid mycorrhizas are found in the dominant plant species of heathland.

#### ectomycorrhizas

In ectomycorrhizas (ECMs), infected roots are usually concentrated in the litter layer of the soil. Fungi form a sheath of varying thickness around the roots. From there, hyphae radiate into the litter layer, extracting nutrients and water and also producing large fruiting bodies that release enormous numbers of wind-borne spores. The fungal mycelium also extends inward from the sheath, penetrating between the cells of the root cortex to give intimate cell-to-cell contact with the host and establishing an interface with a large surface area for the

exchange of the products of photosynthesis, soil water and nutrients between the host plant and its fungal partner.

The ECM fungi are effective in extracting the sparse and patchy supplies of phosphorus and especially nitrogen from the forest litter layer. Carbon flows from the plant to the fungus, very largely in the form of simple hexose sugars: glucose and fructose. Fungal consumption of these may represent up to 30% of the plants' net rate of photosynthate production. The plants, though, are often nitrogen-limited, since in forest litter there are low rates of nitrogen mineralization (conversion from organic to inorganic forms), and inorganic nitrogen is itself mostly available as ammonia. It is therefore crucial for forest trees that ECM fungi can access organic nitrogen directly through enzymic degradation, and utilize ammonium as a preferred source of inorganic nitrogen. Nonetheless, the idea that this relationship between the fungi and their host plants is mutually exploitative rather than 'cosy' is emphasized by its responsiveness to changing circumstances. ECM growth is directly related to rate of flow of hexose sugars from the plant. But when the direct availability of nitrate to the plants is high, either naturally or through artificial supplementation, plant metabolism is directed away from hexose production (and export) and towards amino acid synthesis. As a result the ECM degrades: the plants seem to support just as much ECM as they appear to need.

Arbuscular mycorrhizas (AMs) do not form a sheath but penetrate *within* the roots of the host. Roots become infected from mycelium present in the soil or from germ tubes that develop from asexual spores, which are very large and produced in small numbers: a striking contrast with the ECM fungi. Initially, the fungus grows between host cells but then enters them and forms a finely branched intracellular 'arbuscule'.

There has been a tendency to emphasize facilitation of the uptake of phosphorus as the main benefit to plants from AM symbioses (phosphorus is a highly immobile element in the soil, and is therefore frequently limiting to plant growth), but the truth appears to be more complex than this, with benefits demonstrated, too, in nitrogen uptake, pathogen and herbivore protection, and resistance to toxic metals (Newsham et al., 1995). Certainly, there are cases where the inflow of phosphorus is strongly related to the degree of colonization of roots by AM fungi. This has been shown for the bluebell, *Hyacinthoides non-scripta*, as colonization progresses during its phase of subterranean growth from August to February through to its above-ground photosynthetic phase thereafter (Figure 8.14a). Indeed, bluebells cultured without AM fungi are unable to take up phosphorus through their poorly branched system of roots (Merryweather & Fitter, 1995).

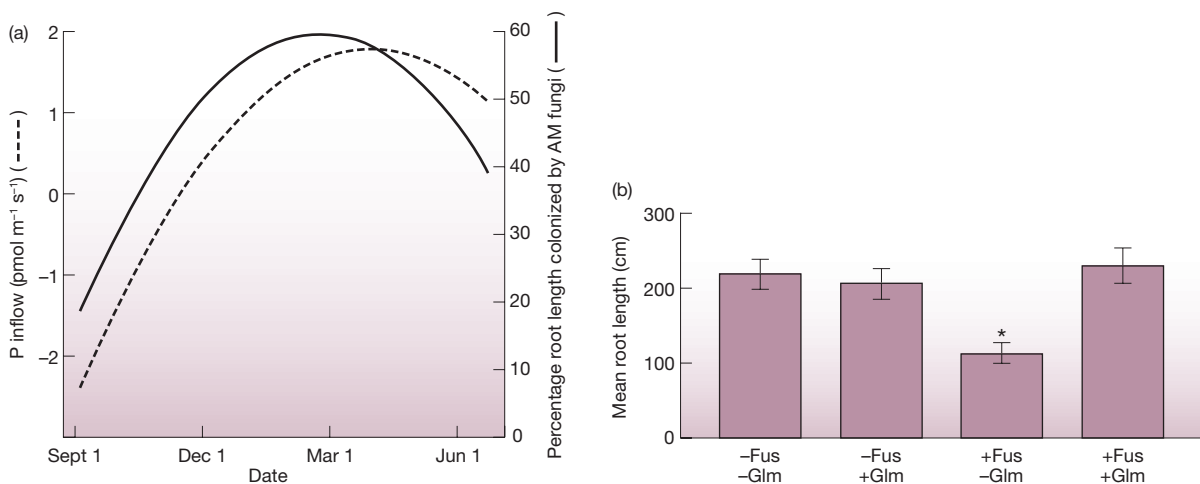
On the other hand, a set of experiments examined the growth of the annual grass *Vulpia ciliata* ssp. *ambigua* (Figure 8.14b) in which seedlings of *Vulpia* were grown with an AM fungus (*Glomus* sp.), with the pathogenic fungus *Fusarium oxysporum*, with both, and with neither. Growth was not enhanced by *Glomus* alone, but growth was harmed by *Fusarium* in the absence of *Glomus*. When both were present, growth returned to normal levels. Clearly, the mycorrhiza did not benefit the phosphorus economy of the *Vulpia*, but it did protect it from the harmful effects of the pathogen.

The key difference appears to be that *Vulpia*, unlike the bluebell, has a highly branched system of roots (Newsham et al., 1995). Plants with finely branched roots have little need for supplementary phosphorus capture, but development of that

arbuscular mycorrhizas

a range of benefits?

it depends on the species



**Figure 8.14**

(a) Curves fitted to rates of phosphorus inflow (dashed line, left axis) and root colonization by arbuscular mycorrhiza (AM) fungi (solid line, right axis) in the bluebell, *Hyacinthoides non-scripta*, over a single growing season. Phosphorus uptake appears to be strongly linked to root colonization by the fungi. (b) The effects of a factorial combination of *Fusarium oxysporum* (Fus, a pathogenic fungus) and an AM fungus, *Glomus* sp. (Glm) on growth (root length) of *Vulpia* plants. Values are means of 16 replicates per treatment; bars are standard errors; the asterisk signifies a significant difference at  $P < 0.05$  in a Fisher's pairwise comparison. In this case, the benefit provided by AM fungi seems not to be an improvement in nutrient uptake but protection against the pathogen.

(A) AFTER MERRYWEATHER & FITTER, 1995; NEWSHAM ET AL., 1995; (B) AFTER NEWSHAM ET AL., 1994, 1995

same root architecture provides multiple points of entry for plant pathogens. In such cases AM symbioses are therefore likely to have evolved with an emphasis on plant protection. By contrast, root systems with few lateral and actively growing meristems are relatively invulnerable to pathogen attack, but these root systems are poor foragers for phosphorus. Here, AM symbioses are likely to have evolved with an emphasis on phosphorus capture.

#### 8.4.6 Fixation of atmospheric nitrogen in mutualistic plants

The inability of most plants and animals to fix atmospheric nitrogen is one of the great puzzles in the process of evolution, since nitrogen is in limiting supply in many habitats. However, the ability to fix nitrogen is widely though irregularly distributed amongst both the eubacteria ('true' bacteria) and the archaea (Archaeobacteria), and many of these have been caught up in tight mutualisms with distinct groups of eukaryotes. The best known, because of the huge agricultural importance of legume crops, are the rhizobia, which fix nitrogen in the root nodules of most leguminous plants and just one non-legume, *Parasponia* (a member of the family Ulmaceae, the elms).

The establishment of the liaison between rhizobia and legume plants proceeds by a series of reciprocating steps. The bacteria occur in a free-living state in the soil and are stimulated to multiply by root exudates and cells that have been sloughed from roots as they develop. In a typical case, a bacterial colony develops

mutualisms of rhizobia and leguminous plants: several steps to a liaison



on the root hair, which then begins to curl and is penetrated by the bacteria. The host responds by laying down a wall that encloses the bacteria and forms an ‘infection thread’, which grows within the host root cortex, and within which the rhizobia proliferate. Rhizobia in the infection thread cannot fix nitrogen, but some are released into host cells in a developing ‘nodule’, where, surrounded by a host-derived peribacteroid membrane, they differentiate into ‘bacteroids’ that can fix nitrogen. Meanwhile, a special vascular system develops in the host, supplying the products of photosynthesis to the nodule tissue and carrying away fixed-nitrogen compounds to other parts of the plant.

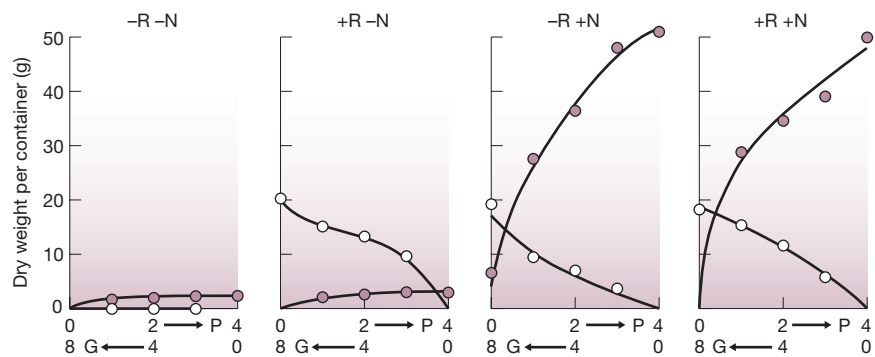
The costs and benefits of this mutualism need to be considered carefully. From the plant’s point of view, we need to compare the energetic costs of alternative processes by which supplies of fixed nitrogen might be obtained. The route for most plants is direct from the soil as nitrate or ammonium ions. The metabolically cheapest route is the use of ammonium ions, but in most soils ammonium ions are rapidly converted to nitrates by microbial activity (nitrification). The energetic cost of reducing nitrate from the soil to ammonia is about 12 mol of adenosine triphosphate (ATP, the cell’s energy currency) per mole of ammonia formed. The mutualistic process (including the maintenance costs of the bacteroids) is energetically slightly more expensive to the plant: about 13.5 mol of ATP. However, we must also add the costs of forming and maintaining the nodules, which may be about 12% of the plant’s total photosynthetic output. It is this that makes nitrogen fixation energetically inefficient. Energy, though, may be much more readily available for green plants than nitrogen. A rare and valuable commodity (fixed nitrogen) bought with a cheap currency (energy) may be no bad bargain. On the other hand, when a nodulated legume is provided with nitrates (i.e. when nitrate is *not* a rare commodity) nitrogen fixation declines rapidly.

On the other hand, the mutualisms of rhizobia and legumes (and other nitrogen-fixing mutualisms) must not be seen as isolated interactions between bacteria and their own host plants. In nature, legumes normally form mixed stands in association with non-legumes. These are potential competitors with the legumes for fixed nitrogen (nitrates or ammonium ions in the soil). The nodulated legume sidesteps this competition by its access to its unique source of nitrogen. It is in this ecological context that nitrogen-fixing mutualisms gain their main advantage. Where nitrogen is plentiful, however, the energetic costs of nitrogen fixation often put the plants at a competitive *dis*advantage.

Figure 8.15, for example, shows the results of a classic experiment in which soybeans (*Glycine soja*, a legume) were grown in mixtures with *Paspalum*, a grass. The mixtures either received mineral nitrogen, or were inoculated with *Rhizobium*, or received both. The experiment was designed as a ‘replacement series’, which allows us to compare the growth of pure populations of the grass and legume with their performances in the presence of each other. In the pure stands of soybean, yield was increased very substantially *either* by inoculation with *Rhizobium*, *or* by application of fertilizer nitrogen, or by receiving both. The legumes can use either source of nitrogen as a substitute for the other. The grass, however, responded only to the fertilizer. Hence, when the species competed in the presence of *Rhizobium* alone, the legume contributed far more to the overall yield than did the grass: over a succession of generations, the legume would have outcompeted the grass. When they competed in soils supplemented

costs and benefits of rhizobial mutualisms

interspecific competition:  
a classic ‘replacement series’



**Figure 8.15**

The growth of soybeans (*Glycine soja*, G, ○) and a grass (*Paspalum*, P, ●) grown alone and in mixtures with and without nitrogen fertilizer (N) and with and without inoculation with nitrogen-fixing *Rhizobium* (R). The plants were grown in pots containing 0–4 plants of the grass together with 0–8 plants of *Glycine*. Thus, moving left to right on the horizontal axis, the treatments are zero *Paspalum* (0P) and 8 *Glycine* (8G), 1P with 6G, 2P with 4G, 3P with 2G and, finally, 4P with 0G. The vertical scale on each figure shows the mass of plants of the two species in each container. –R –N, no *Rhizobium* and no fertilizer; +R –N, inoculated with *Rhizobium* but no fertilizer; –R +N, no *Rhizobium* but nitrate fertilizer was applied; +R +N, inoculated with *Rhizobium* and nitrate fertilizer was supplied. When the two species competed in the presence of nitrogen-fixing *Rhizobium* and without fertilizer, the soybeans (with their mutualistic relationship to *Rhizobium*) performed best, but in the presence of nitrogen fertilizer (with or without the *Rhizobium*) the grass outperformed the soybeans.

After de Wit et al., 1966

the shifting balance between  
nitrogen-fixers and non-fixers

with fertilizer nitrogen, however, whether or not *Rhizobium* was also present, it was the grass that made the major contribution: long term, it would have out-competed the legume.

Quite clearly, then, it is in environments deficient in nitrogen that nodulated legumes have a great advantage over other species. But their activity raises the level of fixed nitrogen in the environment. After death, legumes augment the level of soil nitrogen on a very local scale with a 6–12-month delay as they decompose. Thus, their advantage is lost – they have improved the environment of their competitors, and the growth of associated grasses will be favored in these local patches. Hence, organisms that can fix atmospheric nitrogen can be thought of as locally suicidal. This is one reason why it is very difficult to grow repeated crops of pure legumes in agricultural practice without aggressive grass weeds invading the nitrogen-enriched environment. It may also explain why leguminous herbs or trees usually fail to form dominant stands in nature.

Grazing animals, on the other hand, continually remove grass foliage, and the nitrogen status of a grass patch may again decline to a level at which the legume is once more at a competitive advantage. In a stoloniferous legume, such as white clover, the plant is continually ‘wandering’ through the sward, leaving behind it local grass-dominated patches, whilst invading and enriching with nitrogen new patches where the nitrogen status has become low. The symbiotic legume in such a community not only drives its nitrogen economy but also some of the cycles that occur within its patchwork (Cain et al., 1995).

We end this section, then, on a theme that has recurred repeatedly. To understand the ecology of mutualistic pairs, we must look beyond those species to the wider community of which they are part.



## Summary

# SUMMARY

### Molecular ecology: differentiation within and between species

For much of the time, it is entirely appropriate for ecologists to talk about 'populations' or 'species' as if they were singular, homogeneous entities, but for some purposes, knowing how much differentiation there is within species, or between one species and another, is critical for an understanding of their dynamics, and ultimately for managing those dynamics. Molecular genetic markers, of a variety of types, have massively increased the resolution at which we can differentiate between populations and even individuals.

Studies on albatrosses illustrate how even within a species of conservation importance, separate populations even more threatened with extinction may be hidden; while studies on salmon illustrate how molecular markers can be used to detect, and to prosecute, illegal fishermen. Molecular markers have also shown, for example, that a threatened 'species', the red wolf, may in fact be a hybrid between two other, relatively common species, with implications for both the desirability and the practicality of its conservation.

### Coevolutionary arms races

A better defended food resource exerts a selection pressure on consumers to overcome that defense. A consumer that does so will steal a march on its competitors, and so is likely to become relatively specialized on that prey type – which is then under particular pressure to defend itself against that particular consumer, and so on: a coevolutionary 'arms race'. Plants relying on toxins are more prone to becoming involved in arms races with their herbivores than those relying on more 'quantitative' (digestion-reducing) chemicals.

The intimate association between parasites and their hosts makes them especially prone to coevolutionary arms races. However, the process is not necessarily so straightforward, as illustrated by the case of the myxoma virus and the European rabbit. The evolution of resistance in the rabbit is easy to understand, but the parasites favored by natural selection are those with the greatest reproductive rate.

In the myxoma virus, this occurs at intermediate levels of virulence because of increased transmissibility.

In other cases, host–parasite coevolution is more definitely antagonistic: increasing resistance in the host and increasing infectivity in the parasite. With bacteria and their viruses, this process can be observed in action, because generation times are so short.

### Mutualistic interactions

No species lives in isolation, but often the association with other species is especially close: for many organisms, the habitat they occupy is an individual of another species – a symbiosis. A mutualistic relationship is one in which organisms of different species interact to their mutual benefit. Current evolutionary thinking views mutualisms as cases of reciprocal exploitation where nonetheless each partner is a *net* beneficiary. Mutualisms themselves have often been neglected in the past compared to other types of interaction, yet mutualists compose most of the world's biomass.

Pairs of species from many taxa take part in mutualistic associations in which one species protects the other from predators or competitors but gains privileged access to a food resource on the protected species.

Some of the most dramatic mutualisms are those of human agriculture, but similar 'farming' mutualisms have developed in termite and especially ant societies. Ants farm many species of aphids in return for sugar-rich secretions of honeydew. The aphids benefit through suffering lower mortality rates; but there are also costs: where aphid predators are excluded experimentally, aphids grow less well in the presence of ants.

Very many plant species use animals to disperse their seeds and pollen, and many different kinds of animals have entered into pollination liaisons with flowering plants. The pollinators par excellence, though, are the insects.

The gastrointestinal tracts of all vertebrates are populated by a mutualistic microbiota. The microbes receive a steady flow of substrates for growth in the form of food that has been eaten, and they live within a chamber in which pH and, in endotherms, temperature

are regulated and anaerobic conditions are maintained. The vertebrate hosts receive nutrition from food that they would otherwise find, literally, indigestible.

Most higher plants do not have roots, they have mycorrhizas – intimate mutualisms between fungi and root tissue. In ectomycorrhizas (ECMs), fungi form a sheath of varying thickness around the roots. These fungi are effective in extracting the sparse and patchy supplies of phosphorus and especially nitrogen from the forest litter layer. Carbon flows from the plant to the fungus (mostly hexose sugars). However, ECM growth is directly related to the rate of flow of the sugars from the plant. When the direct availability of nitrate to the plants is high, plant metabolism is directed away from hexose production. As a result the ECM degrades: the plants seem to support just as much ECM as they appear to need. Arbuscular mycorrhizas (AMs) penetrate *within* the roots of the host. There has been

a tendency to emphasize facilitation of the uptake of phosphorus as the main benefit to plants from AM symbioses, but benefits have been demonstrated, too, in nitrogen uptake, pathogen and herbivore protection, and resistance to toxic metals.

The ability to fix nitrogen is widely distributed amongst both the eubacteria and the Archaeobacteria, and many of these have been caught up in tight mutualisms with distinct groups of eukaryotes. The best known are the rhizobia, which fix nitrogen in the root nodules of most leguminous plants. Nitrogen fixation is often energetically inefficient, but energy may be much more readily available for green plants than nitrogen. On the other hand, when a nodule legume is provided with nitrates, nitrogen fixation declines rapidly. The mutualisms of rhizobia and legumes (like other nitrogen-fixing mutualisms) must be seen in the context of competition between legumes and non-legumes.

## Review questions

### REVIEW QUESTIONS

Asterisks indicate challenge questions

- 1 Explain why molecular (DNA) markers have improved the ability of ecologists to study degrees of differentiation within and between species.
- 2\* Review the range of molecular markers that have been used in molecular ecology, stressing their advantages and disadvantages at different scales of resolution.
- 3 Should the red wolf be conserved, or would that be a misguided waste of public money?
- 4 Why are some plants more likely than others to be involved in arms races with their insect herbivores?
- 5 Account for the decline in virulence of the myxomatosis virus in European rabbits after its initial introductions in Australia and Europe.
- 6 Compare and contrast the mutualistic associations of ants with plants they protect and aphids they farm.
- 7\* Discuss the following propositions: 'Most herbivores are not really herbivores but consumers of the byproducts of the mutualists living in their gut' and 'Most gut parasites are not really parasites but competitors with their hosts for food that the host has captured'.
- 8 Compare the roles of fruits and nectar in the interactions between plants and the animals that visit them.
- 9 What are mycorrhizas and what is their significance?
- 10\* Leguminous plants are a perfect example of a mutualistic association that can only be understood in the context of the ecological community within which it normally exists. Discuss.

# Chapter 9



## From populations to communities

### *Chapter contents*

#### CHAPTER CONTENTS

- 9.1 Introduction
- 9.2 Multiple determinants of the dynamics of populations
- 9.3 Dispersal, patches and metapopulation dynamics
- 9.4 Temporal patterns in community composition
- 9.5 Food webs

### *Key concepts*

#### KEY CONCEPTS

In this chapter you will:

- appreciate the variety of interacting abiotic and biotic factors that account for the dynamics of populations
- distinguish between the determination and regulation of population abundance
- understand how patchiness and dispersal between patches influence the dynamics of both populations and communities
- recognize the influence of disturbance on community patterns and understand the nature of community succession
- appreciate the importance of direct and indirect effects and distinguish between bottom-up and top-down control of food webs
- understand the relationship between the structure and stability of food webs

*In previous chapters, we generally dealt with individual species or pairs of species in isolation, as ecologists often do. Ultimately, however, we must recognize that every population exists within a web of interactions with myriad other populations, across several trophic levels. Each population must be viewed in the context of the whole community, and we need to understand that populations occur in patchy and inconstant environments in which disturbance and local extinction may be common.*

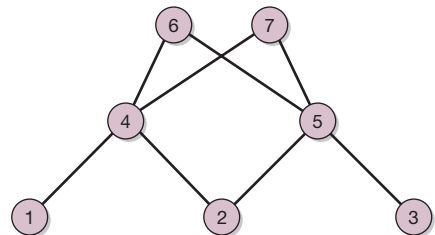
## 9.1 Introduction

Single-species populations have been the focus for many of the questions posed in previous chapters. In attempting to answer the most fundamental ecological question of all – what determines a species' abundance and distribution – we have chosen to ask separately about the role of conditions and resources, of migration, of competition (both intra- and interspecific), of mutualism, and of predation and parasitism. In reality, the dynamics of any population reflect a combination of these effects, though their relative importance varies from case to case. Now, therefore, we need to view the population in the context of the whole community, since each exists within a whole web of interactions (Figure 9.1), and each responds differently to the prevailing abiotic conditions.

In Section 9.2 we consider how abiotic and biotic factors combine to determine the dynamics of species populations. Then, in Section 9.3, we revisit one of the major themes of this book – the importance of patchiness and dispersal between patches in ecological dynamics – and discuss especially the importance of the concept of the metapopulation. Disturbances, such as forest fires and the storm battering of seashores, also play an important role in the dynamics of many populations and the composition of most communities. After each disturbance, there is a pattern of re-establishment of species that is played out against a background of changing conditions, resources and population interactions. We deal with temporal patterns in community composition, including community succession, in Section 9.4. Finally, in Section 9.5 we broaden our view further to examine food webs, like the one illustrated in Figure 9.1, with usually at least

**Figure 9.1**

Community matrix illustrating how each species may interact with several others in competitive interactions (among plant species 1, 2 and 3; or between grazers 4 and 5; or between predators 6 and 7) and predator–prey interactions (such as between 6 and 4, or 5 and 2).





three trophic levels (plant–herbivore–predator), emphasizing the importance not only of direct but also of indirect effects that a species may have on others on the same trophic level or on levels below or above it.

## 9.2 Multiple determinants of the dynamics of populations

Why are some species rare and others common? Why does a species occur at low population densities in some places and at high densities in others? What factors cause fluctuations in a species' abundance? These are crucial questions when we wish to conserve rare species, or control pests, or manage natural, living resources, or when we wish simply to understand the patterns and dynamics of the natural world. To provide complete answers for even a single species in a single location, we need to know the physicochemical conditions, the level of resources available, the organism's life cycle and the influence of competitors, predators, parasites and so on – and how all these factors influence abundance through effects on birth, death, dispersal and migration. We now bring these factors together and consider how we might discover which actually matter in particular examples.

The raw material for the study of abundance is usually some estimate of the numbers of individuals in a population. However, a record of numbers alone can hide vital information. Picture three human populations, shown to contain identical numbers of individuals. One is an old people's residential area, the second is a population of young children and the third is a population of mixed age and sex. In the absence of information beyond mere numbers, it would not be clear that the first population was doomed to extinction (unless maintained by immigration), the second would grow fast but only after a delay and the third would continue to grow steadily. The most satisfactory studies, therefore, estimate not only the numbers of individuals (and their parts, in the case of modular organisms) but also those of different age, sex and size.

The data that accumulate from estimates of abundance may be used to establish correlations with external factors like food or weather. Correlations may be used to predict the future. For example, high intensities of the disease 'late blight' in potato crops usually occur 15–22 days after a period in which the minimum temperature is above 10°C and relative humidity is more than 75% for two consecutive days. Such a correlation may alert the potato grower to the need for protective spraying. Correlations may also suggest – but not prove – causal relationships. For example, a correlation may be demonstrated between the size of a population and its growth rate. But ultimately 'cause' requires a mechanism. When the population is large, many individuals may starve to death, or may fail to reproduce, or may become aggressive and drive out the weaker members. A correlation cannot tell us which. Nonetheless, correlations can be informative. Figure 9.2, for example, shows four examples in which population growth rate increases with the availability of food. It also suggests that in general, such relationships are likely to level off at the highest food levels where some other factor or factors place an upper limit on abundance.

fluctuations in abundance are caused by a wide variety of biotic and abiotic factors

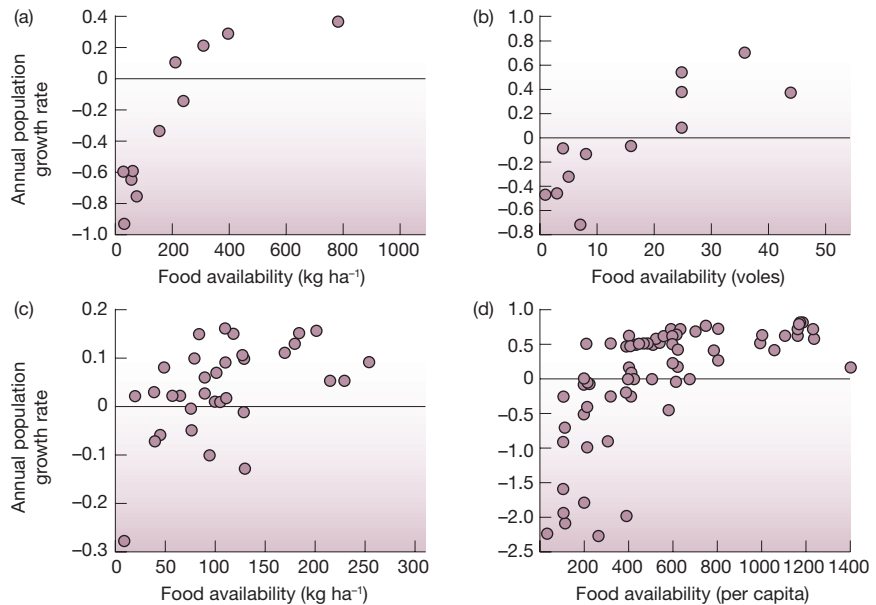
what total numbers can and cannot tell us

what correlations can and cannot tell us



## Figure 9.2

Increases in annual population growth rate with the availability of food, measured as pasture biomass ( $\text{kg ha}^{-1}$ ) in (a) and (c), as vole abundance in (b) and as availability of food per capita in (d). (a) Red kangaroo (Bayliss, 1987). (b) Barn owl (modified from Taylor, 1994). (c) Wildebeest (Krebs et al., 1999). (d) Feral pig (Choquenot, 1998). Positive growth rates indicate increasing abundance; negative growth rates decreasing abundance.



AFTER SIBLY & HONE, 2002

### 9.2.1 Fluctuation or stability?

many populations are  
very stable . . .

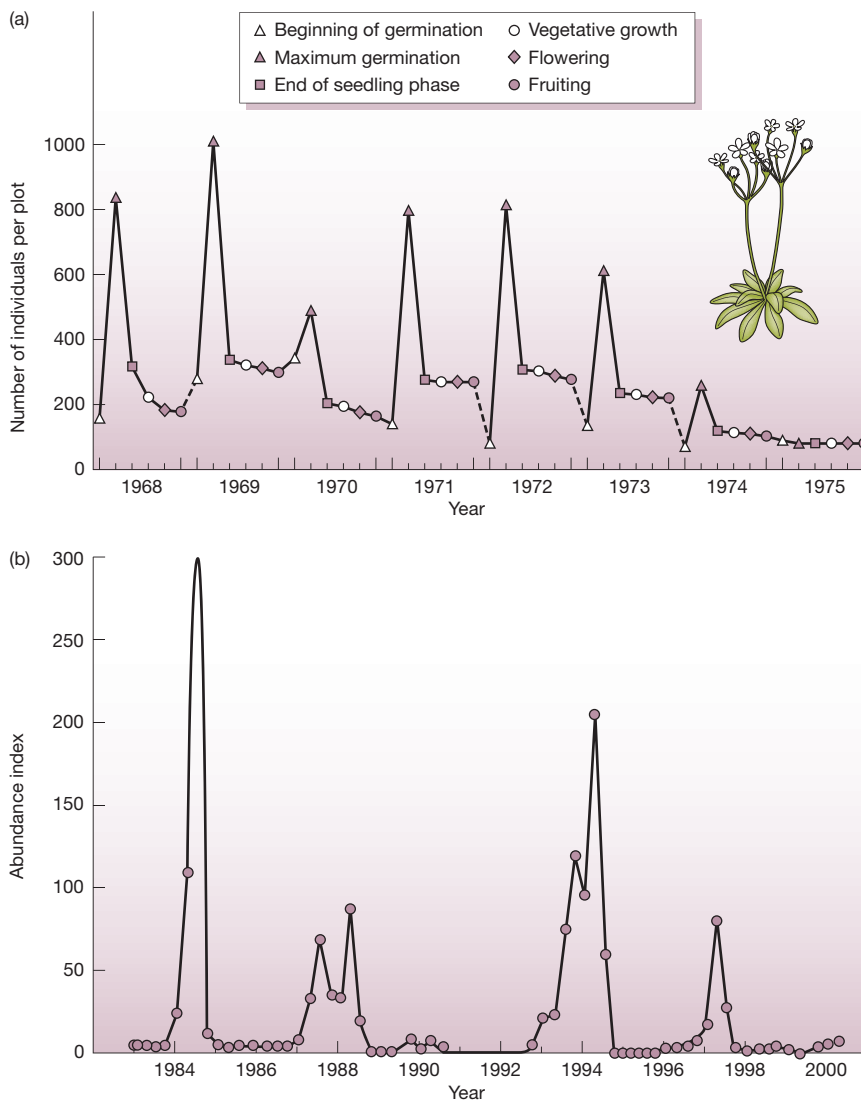
Some populations appear to change very little in size. One study that covered an extended timespan – though it was not necessarily the most scientific – examined swifts (*Microtus apus*) in the village of Selborne in southern England over more than 200 years. In one of the earliest published works on ecology, Gilbert White, who lived in the village, wrote in 1778 (see White, 1789):

I am now confirmed in the opinion that we have every year the same number of pairs invariably. . . . The number that I constantly find are eight pairs, about half of which reside in the church, and the rest in some of the lowest and meanest thatched cottages.

More than 200 years later, Lawton and May (1984) visited the village and, not surprisingly, found major changes. Swifts are unlikely to have nested in the church for 50 years, and the thatched cottages have either disappeared or had their roofs covered with wire. Yet the number of breeding pairs of swifts regularly to be found in the village is now 12. In view of the many changes that have taken place in the intervening centuries, this number is remarkably close to the eight pairs so consistently found by White.

But the stability of a population may conceal complex underlying dynamics. Another example of a population showing relatively little change in adult numbers from year to year is seen in an 8-year study in Poland of the small, annual sand-dune plant *Androsace septentrionalis* (Figure 9.3a). Each year, however, there was great flux within the population. Between 150 and 1000 new seedlings per square meter appeared, but subsequent mortality reduced the population by between 30% and 70%. Thus, the population appears to be kept within bounds. At least 50 plants always survived to fruit and produce seeds for the next season. By contrast, the mice in Figure 9.3b have extended periods of relatively low abundance interrupted by sporadic and dramatic irruptions.

. . . but stability need not mean  
'nothing changes'

**Figure 9.3**

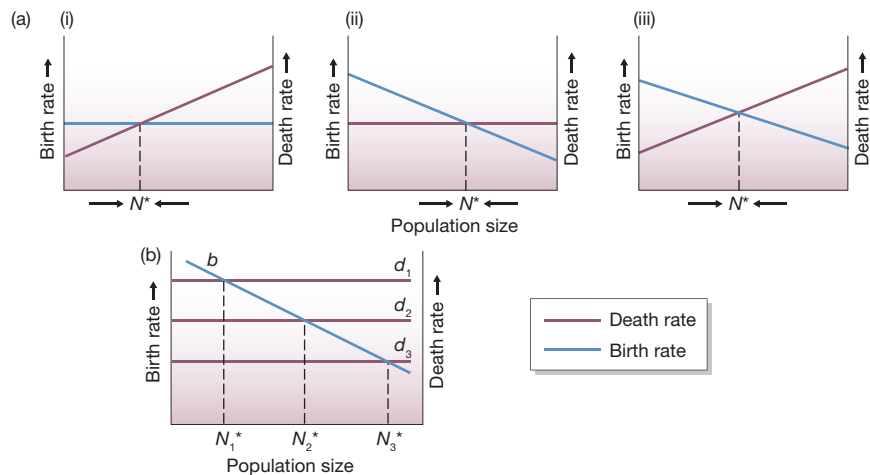
(a) The population dynamics of *Androsace septentrionalis* during an 8-year study. (b) Irregular irruptions in the abundance of house mice (*Mus domesticus*) in an agricultural habitat in Victoria, Australia, where the mice, when they irrupt, are serious pests. The 'abundance index' is the number caught per 100 trap-nights. In the fall of 1984 the index exceeded 300.

(a) AFTER SYMONIDES, 1979; (b) AFTER SINGLETON ET AL., 2001

### 9.2.2 Determination and regulation of abundance

Is the move from eight to 12 pairs of swifts over 200 years an indication of consistency or of change? Is the similarity between eight and 12 of most interest – or the difference between them? Some investigators have emphasized the apparent constancy of populations; others have emphasized the fluctuations.

Those who have emphasized constancy argue that we need to look for stabilizing forces within populations to explain why the populations do not exhibit unfettered increase or a decline to extinction (generally, density-dependent forces: for instance, competition between crowded individuals for limited resources). Those who have emphasized fluctuations often look to external factors, weather or disturbance, to explain the changes. Can the two sides be brought together to form a consensus?



**Figure 9.4**

(a) Population regulation with: (i) density-independent birth and density-dependent death; (ii) density-dependent birth and density-independent death; and (iii) density-dependent birth and death. Population size increases when birth rate exceeds death rate and decreases when death rate exceeds birth rate.  $N^*$  is therefore a stable equilibrium population size. The actual value of the equilibrium population size is seen to depend on both the magnitude of the density-independent rate and the magnitude and slope of any density-dependent processes. (b) Population regulation with density-dependent birth,  $b$ , and density-independent death,  $d$ . Death rates are determined by physical conditions which differ in three sites (death rates  $d_1$ ,  $d_2$  and  $d_3$ ). Equilibrium population size varies as a result ( $N_1^*$ ,  $N_2^*$ ,  $N_3^*$ ).

the distinction between  
determination and regulation

To do so, it is important to understand clearly the difference between questions about the ways in which abundance is *determined* and questions about the way in which abundance is *regulated*. Regulation is the tendency of a population to decrease in size when it is above a particular level, but to increase in size when below that level. In other words, regulation of a population can, by definition, occur only as a result of one or more density-dependent processes (see Chapters 3 and 5) that act on rates of birth and/or death and/or movement (Figure 9.4a). Various potentially density-dependent processes have been discussed in earlier chapters on competition, predation and parasitism. We must look at regulation, therefore, to understand how it is that a population tends to remain within defined upper and lower limits.

On the other hand, the precise abundance of individuals will be determined by the combined effects of all the factors and all the processes that affect a population, whether they are dependent or independent of density (Figure 9.4b). We must look at the determination of abundance, therefore, to understand how it is that a particular population exhibits a particular abundance at a particular time, and not some other abundance.

In the past, certainly, some have believed that density-dependent, biotic interactions play the main role not only in regulating but also in determining population size, holding populations in a state of balance in their environments. Others have felt that most natural populations could be viewed as passing through a repeated sequence of setbacks and recovery. This view tends to reject any subdivision of the environment into density-dependent and density independent 'factors', preferring instead to see populations as sitting at the

center of an ecological web, where various factors and processes interact in their effects on the population.

There is really no conflict between the two views. The first is preoccupied with what regulates population size and the second with what determines population size – and both are perfectly valid interests. No population can be absolutely free of regulation – long-term unrestrained population growth is unknown, and unrestrained declines to extinction are rare. Furthermore, any suggestion that density-dependent processes are rare or generally of only minor importance would be wrong. A very large number of studies have been made of various kinds of animals, especially of insects. Density dependence has by no means always been detected but it is commonly seen when studies are continued for many generations. For instance, density dependence was detected in 80% or more of studies of insects that lasted for more than 10 years (Hassell et al., 1989; Woivod & Hanski, 1992).

On the other hand, for many populations weather is typically the major determinant of abundance and other factors are of relatively minor importance. For instance, in one famous, classic study of a pest, apple thrips, weather accounted for 78% of the variation in the number of thrips (Davidson & Andrewartha, 1948); for predicting thrips' abundance, information on the weather is of paramount importance. So, what regulates the size of a population need not determine its size for most of the time. It would be wrong to give regulation or density dependence some kind of pre-eminence. It may be occurring only infrequently or intermittently, and it is likely that no natural population is ever truly at equilibrium: even when regulation is occurring, it may be drawing abundance toward a level that is itself changing in response to changing levels of resources. Thus, there are a range of possibilities: some populations in nature are almost always recovering from the last disaster (Figure 9.5a), others are usually limited by an abundant resource (Figure 9.5b) or by a scarce resource (Figure 9.5c), and others are usually in decline after sudden episodes of colonization (Figure 9.5d).

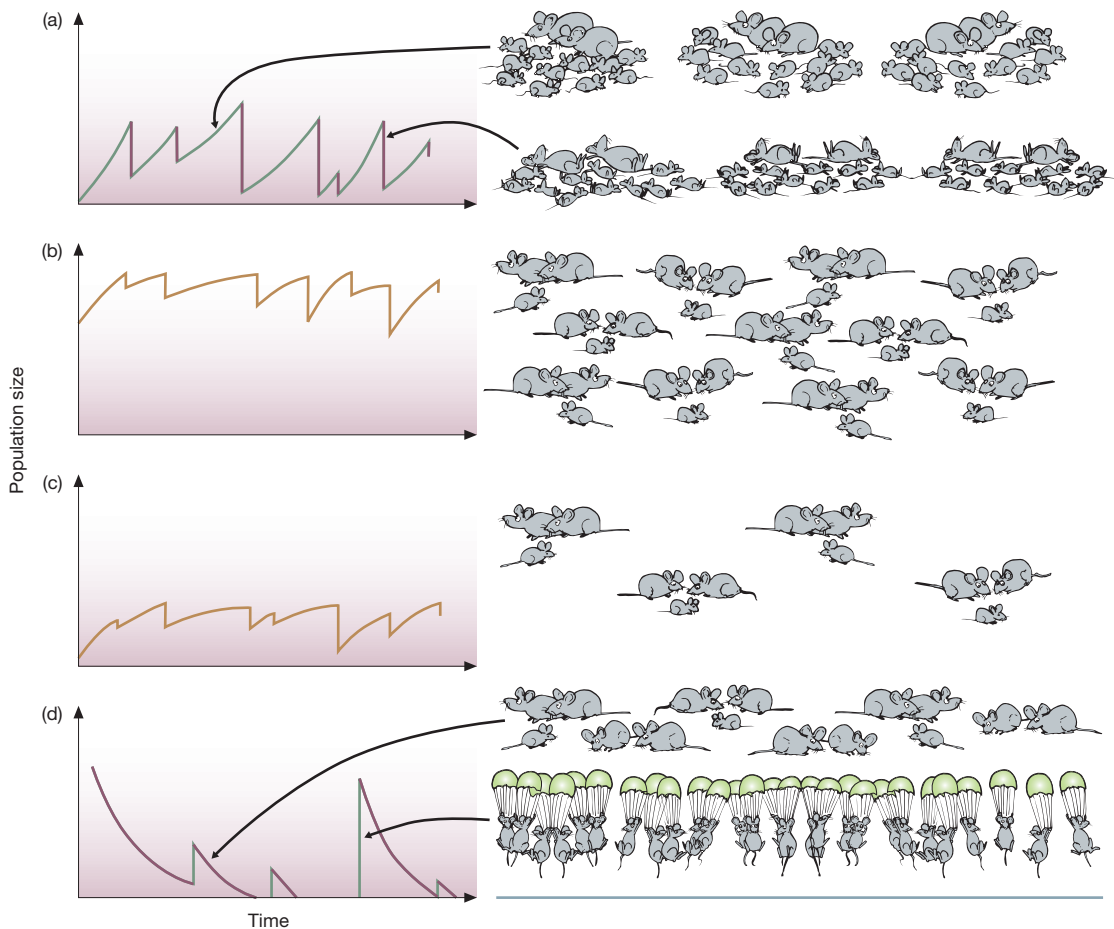
both are perfectly valid interests

### 9.2.3 Key factor analysis

We can distinguish clearly between what regulates and what determines the abundance of a population, and see how regulation and determination relate to one another, by examining an approach known as *key factor analysis*. It has been applied to many insects and some other animals and plants and is based on calculating what are known as *k*-values for each phase of the life cycle. In fact, key factor analysis is poorly named, since it identifies key *phases* (rather than key factors) in the life of a study organism (those most important in determining abundance). Details are described in Box 9.1, but the approach can be understood simply by appreciating that the *k*-values measure the amount of mortality: the higher the *k*-value, the greater the mortality (*k* stands for 'killing power').

For a key factor analysis to be carried out, data are compiled in the form of a life table (see Chapter 5), such as that done for a Canadian population of the Colorado potato beetle (*Leptinotarsa decemlineata*) in Box 9.1. The sampling program in that case provided estimates of the population at seven stages: eggs, early larvae, late larvae, pupae, summer adults, hibernating adults and spring adults. One further category was included, females  $\times 2$ , to take account of any unequal sex ratios among the summer adults.

Colorado potato beetles



**Figure 9.5**

Idealized diagrams of population dynamics: (a) dynamics dominated by phases of population growth after disasters; (b) dynamics dominated by limitations on environmental carrying capacity, where the carrying capacity is high; (c) same as (b) but where the carrying capacity is low; (d) dynamics within a habitable site dominated by population decay after more or less sudden episodes of colonization or recruitment.



## 9.1 Quantitative aspects

### 9.1 QUANTITATIVE ASPECTS

#### Determining $k$ -values for key factor analysis

Table 9.1 sets out a typical set of life table data, collected by Harcourt (1971) for the Colorado potato beetle, *Leptinotarsa decemlineata*, in Canada. The first column lists the various phases of the life cycle.

*Spring adults* emerge from hibernation around the middle of June, when potato plants are breaking through the ground. Within 3 or 4 days egg laying begins, and it continues for about 1 month. The eggs

**Table 9.1**

Life table data for the Canadian Colorado potato beetle.

AGE INTERVAL	NUMBERS PER 96 POTATO HILLS	NUMBERS DYING	MORTALITY FACTOR	FACTOR $\text{LOG}_{10} N$	$k$ -VALUE	
Eggs	11,799	2,531	Not deposited	4.072	0.105	$(k_{1a})$
	9,268	445	Infertile	3.967	0.021	$(k_{1b})$
	8,823	408	Rainfall	3.946	0.021	$(k_{1c})$
	8,415	1,147	Cannibalism	3.925	0.064	$(k_{1d})$
	7,268	376	Predators	3.861	0.023	$(k_{1e})$
Early larvae	6,892	0	Rainfall	3.838	0	$(k_2)$
Late larvae	6,892	3,722	Starvation	3.838	0.337	$(k_3)$
Pupal cells	3,170	16	Parasitism	3.501	0.002	$(k_4)$
Summer adults	3,154	-126	Sex (52% ♀)	3.499	-0.017	$(k_5)$
Females $\times 2$	3,280	3,264	Emigration	3.516	2.312	$(k_6)$
Hibernating adults	16	2	Frost	1.204	0.058	$(k_7)$
Spring adults	14			1.146		
					2.926	$(k_{\text{total}})$

are laid in clusters (approximately 34 eggs) on the lower leaf surface, and the larvae crawl to the top of the plant, where they feed throughout their development, passing through four stages. When mature,



An adult Colorado potato beetle (*Leptinotarsa decemlineata*) taking off from its host plant. Emigration by summer adults represents the key phase in the population dynamics of potato beetles.

they drop to the ground and form pupal cells in the soil. *Summer adults* emerge in early August, feed, and then re-enter the soil at the beginning of September to hibernate and become the next season's spring adults.

The next column lists the estimated numbers (per 96 potato hills) at the start of each phase, and the third column then lists the numbers dying in each phase, before the start of the next. This is followed, in the fourth column, by what were believed to be the main causes of deaths in each stage of the life cycle. The fifth and sixth columns then show how  $k$ -values are calculated. In the fifth column, the logarithms of the numbers at the start of each phase are listed. The  $k$ -values in the sixth column are then simply the differences between successive values in column 5. Thus, each value refers to deaths in one of the phases, and, similarly to column 3, the total of the column refers to the total death throughout the life cycle. Moreover, each  $k$ -value measures the rate or intensity of mortality in its own phase, whereas this is not true for the values in column 3 – there, values tend to be higher earlier in the life cycle simply because there are more individuals 'available' to die. These useful characteristics of  $k$ -values are put to use in *key factor analysis*.

**Table 9.2**

Summary of the life table analysis for Canadian Colorado beetle populations (see Box 9.1).

		MEAN	COEFFICIENT OF REGRESSION ON $k_{\text{TOTAL}}$
Eggs not deposited	$k_{1a}$	0.095	-0.020
Eggs infertile	$k_{1b}$	0.026	-0.005
Rainfall on eggs	$k_{1c}$	0.006	0.000
Eggs cannibalized	$k_{1d}$	0.090	-0.002
Egg predation	$k_{1e}$	0.036	-0.011
Larvae 1 (rainfall)	$k_2$	0.091	0.010
Larvae 2 (starvation)	$k_3$	0.185	0.136
Pupae (parasitism)	$k_4$	0.033	-0.029
Unequal sex ratio	$k_5$	-0.012	0.004
Emigration	$k_6$	1.543	0.906
Frost	$k_7$	0.170	0.010
	$k_{\text{total}}$	2.263	

AFTER HARCOURT, 1971

when does most mortality  
occur?

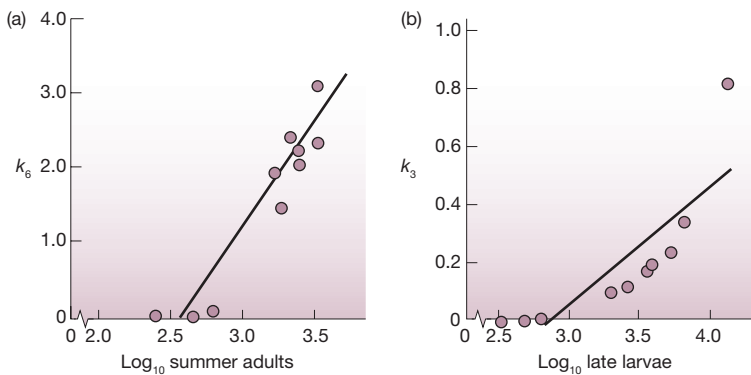
The first question we can ask is: ‘How much of the total “mortality” tends to occur in each of the phases?’ (Mortality is in inverted commas because it refers to all losses from the population.) The question can be answered by calculating the mean  $k$ -values for each phase, in this case determined over 10 seasons (that is, from 10 tables like the one in Box 9.1). These are presented in the third column of Table 9.2. Thus, here, most loss occurred amongst summer adults – in fact, mostly through emigration rather than mortality as such. There was also substantial loss of older larvae (starvation), of hibernating adults (frost-induced mortality), of young larvae (rainfall) and of eggs (cannibalization and ‘not being laid’).

the phases that determine  
abundance . . .

It is usually more valuable, however, to ask a second question: ‘What is the relative importance of these phases as determinants of year-to-year *fluctuations* in mortality, and hence of year-to-year fluctuations in abundance?’ This is rather different. For instance, a phase might repeatedly witness a significant toll being taken from a population (a high mean  $k$ -value), but if that toll is always roughly the same, it will play little part in determining the particular rate of mortality (and thus the particular population size) in any particular year. In other words, this second question is much more concerned with discovering what *determines* particular abundances at particular times, and it can be addressed in the following way.

Mortality during a phase that is important in determining population change – referred to as a *key phase* – will vary in line with total mortality in terms of both size and direction. It is a key phase in the sense that when mortality during it is high, total mortality tends to be high and the population declines – whereas when phase mortality is low, total mortality tends to be low and the population tends to remain large, and so on. By contrast, a phase with a  $k$ -value that varies quite randomly with respect to total  $k$  will, by definition, have little influence on changes in mortality and hence little influence on population size. We need therefore to measure the relationship between phase mortality and total mortality, and this is achieved by the *regression coefficient* of the former on the latter. The largest regression coefficient will be associated with the key phase causing population change, whereas phase mortality that varies at random with total mortality will generate a regression coefficient close to zero.



**Figure 9.6**

(a) Density-dependent emigration by Colorado beetle summer adults (slope = 2.65).  
 (b) Density-dependent starvation of larvae (slope = 0.37).

In the present example (Table 9.2), the summer adults, with a regression coefficient of 0.906, are the key phase. Other phases (with the possible exception of older larvae) have a negligible effect on the changes in generation mortality.

What, though, about the possible role of these phases in the *regulation* of the Colorado beetle population? In other words, which, if any, act in a density-dependent way? This can be answered most easily by plotting  $k$ -values for each phase against the numbers present at the start of the phase. For density dependence, the  $k$ -value should be highest (that is, mortality greatest) when density is highest. For the beetle population, two phases are notable in this respect: for both summer adults (the key phase) and older larvae there is evidence that losses are density-dependent (Figure 9.6) and thus a possible role of those losses in regulating the size of the beetle population. In this case, therefore, the phases with the largest role in determining abundance are also those that seem likely to play the largest part in regulating abundance. But as we see next, this is by no means a general rule.

Key factor analysis has been applied to a great many insect populations, but to far fewer vertebrate or plant populations. Examples of these, though, are shown in Table 9.3 and Figure 9.7.

We start with populations of the wood frog (*Rana sylvatica*) in three regions of the United States (Table 9.3). The larval period was the key phase determining abundance in all regions, largely as a result of year-to-year variations in rainfall. In low-rainfall years, the ponds often dry out, reducing larval survival to catastrophic levels. Such mortality, however, was inconsistently related to the size of the larval population (only one of two ponds in Maryland, and only approaching significance in Virginia) and hence it played an inconsistent part in regulating the sizes of the populations. Rather, in two regions it was during the adult phase that mortality was clearly density-dependent (apparently as a result of competition for food) and, indeed, in two regions mortality was also most intense in the adult phase (first data column).

The key phase determining abundance in a Polish population of the sand-dune annual plant *Androsace septentrionalis* (Figure 9.7) were the seeds in the soil. Once again, however, mortality there did not operate in a density-dependent manner, whereas mortality of seedlings (not the key phase) was density-dependent.

Overall, therefore, key factor analysis (its rather misleading name apart) is useful in identifying important phases in the life cycles of study organisms, and useful too in distinguishing the variety of ways in which phases may be important:

... and the factors that regulate abundance

two further examples of key factor analysis

Table 9.3

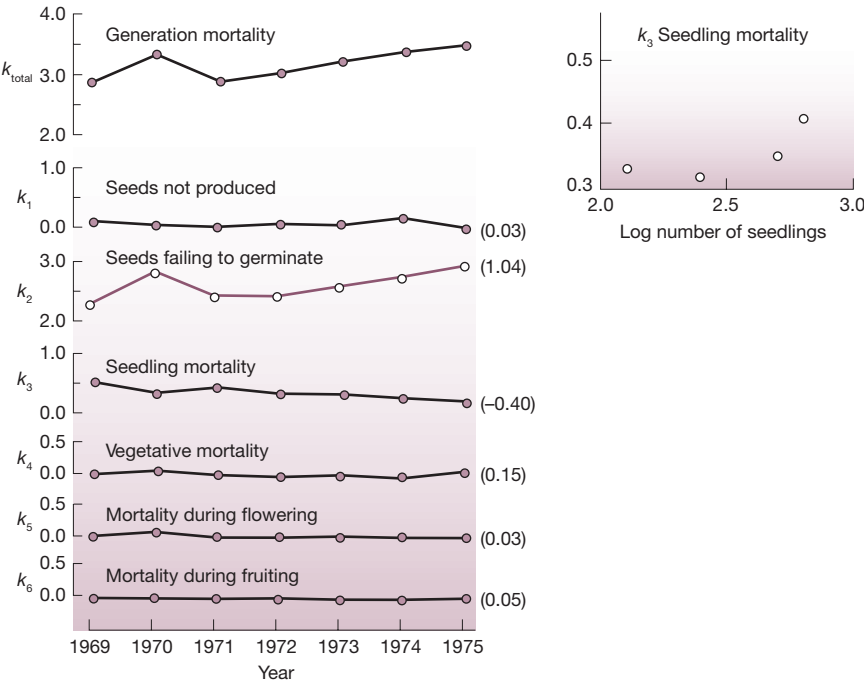
Key factor (or key phase) analysis for wood frog populations in the United States: Maryland (two ponds, 1977–1982), Virginia (seven ponds, 1976–1982) and Michigan (one pond, 1980–1993). In each area, the phase with the highest mean  $k$ -value, the key phase and any phase showing density dependence are highlighted in bold.

AGE INTERVAL	MEAN $k$ -VALUE	COEFFICIENT OF REGRESSION ON $k_{\text{TOTAL}}$	COEFFICIENT OF REGRESSION ON LOG (POPULATION SIZE)
<b>Maryland</b>			
Larval period	1.94	<b>0.85</b>	<b>Pond 1 : 1.03 (<math>P = 0.04</math>)</b> Pond 2 : 0.39 ( $P = 0.50$ )
Juvenile: up to 1 year	0.49	0.05	0.12 ( $P = 0.50$ )
Adult: 1–3 years	<b>2.35</b>	0.10	0.11 ( $P = 0.46$ )
Total	4.78		
<b>Virginia</b>			
Larval period	<b>2.35</b>	<b>0.73</b>	0.58 ( $P = 0.09$ )
Juvenile: up to 1 year	1.10	0.05	−0.20 ( $P = 0.46$ )
Adult: 1–3 years	1.14	0.22	<b>0.26 (<math>P = 0.05</math>)</b>
Total	4.59		
<b>Michigan</b>			
Larval period	1.12	<b>1.40</b>	1.18 ( $P = 0.33$ )
Juvenile: up to 1 year	0.64	1.02	0.01 ( $P = 0.96$ )
Adult: 1–3 years	<b>3.45</b>	−1.42	<b>0.18 (<math>P = 0.005</math>)</b>
Total	5.21		

AFTER BERVEN, 1995

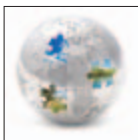
Figure 9.7

Key factor analysis of the sand-dune annual plant *Androsace septentrionalis*. A graph of total generation mortality ( $k_{\text{total}}$ ) and of various  $k$ -factors is presented. The values of the regression coefficients of each individual  $k$ -value on  $k_{\text{total}}$  are given in brackets. The largest regression coefficient signifies the key phase and is shown as a maroon line. The one  $k$ -value that varies in a density-dependent manner.



AFTER SYMONDES, 1979; ANALYSIS IN SILVERTOWN, 1982

in contributing significantly to the overall sum of mortality; in contributing significantly to variations in mortality, and hence in *determining* abundance; and in contributing significantly to the *regulation* of abundance by virtue of the density dependence of the mortality. Box 9.2 presents an account of a topical problem, an understanding of which could benefit from key factor analysis.



## 9.2 Topical ECOncerns

### Acorns, mice, ticks, deer and human disease: complex population interactions

Ecologists have been trying to uncover the complex interactions among acorn production, populations of mice and deer, parasitic ticks and, ultimately, a bacterial pathogen carried by the ticks that can affect people. It is clear that a thorough understanding of the abiotic factors that determine the size of the acorn crop and of the various population interactions can enable scientists to predict years when the risk of human disease is high. This is the topic of the following newspaper article in the *Contra Costa Times* on Friday, February 13, 1998, by Paul Recer.

#### More acorns may mean a rise in Lyme disease

A big acorn crop last fall could mean a major outbreak of Lyme disease next year, according

to a study that linked acorns, mice and deer to the number of ticks that carry the Lyme disease parasite.

Based on the study, researchers at the Institute of Ecosystem Studies in Millbrook, New York, say that 1999 may see a dramatic upswing in the number of Lyme disease cases among people who visit the oak forests of the Northeast.

'We had a bumper crop of acorns this year, so in 1999, two years after the event, we should also have a bumper year for Lyme disease', said Clive G. Jones, a researcher at the Institute of Ecosystem Studies; '1999 should be a year of high risk for Lyme disease'.

Lyme disease is caused by a bacterium carried by ticks. The ticks normally live on mice and deer, but they can bite humans. Lyme disease first causes a mild rash, but left untreated can damage the heart and nervous system and cause a type of arthritis.

Jones, along with researchers at the University of Connecticut, Storrs, and Oregon State University, Corvallis, found that the number of mice, the number of ticks, the deer population and even the number of gypsy moths are linked directly to the production of acorns in the oak forest.

Jones said that in years following a big acorn crop, the number of tick larvae is eight times greater than in years following a poor acorn crop.



Female deer tick (*Ixodes dammini*), which carries Lyme disease ( $\times 7$ ).

© ROBERT CALANTINE, VISUALS UNLIMITED

Additionally, he said, there are about 40 percent more ticks on each mouse.

The researchers tested the effect of acorns by manipulating the population of mice and the availability of acorns in forest plots along the Hudson River. Jones said the work, extended over several seasons, proved the theory that mice and tick populations rise and fall based on the availability of acorns.

(All content © 1998 *Contra Costa Times* and may not be republished without permission. Send comments or questions to [newslib@infi.net](mailto:newslib@infi.net). All archives are stored on a SAVE (tm) newspaper library system from MediaStream Inc., a Knight-Ridder, Inc. company.)

*How could a key factor analysis be used to pinpoint the phases of importance in determining risk of human disease?*

## 9.3 Dispersal, patches and metapopulation dynamics

dispersal is ignored at the ecologist's peril

In many studies of abundance, the assumption has been made that the major events all occur within the study area, and that immigrants and emigrants can safely be ignored. But migration can be a vital factor in determining and/or regulating abundance. We have already seen, for example, that emigration was the predominant reason for the loss of summer adults of the Colorado potato beetle, which was both the key phase in determining population fluctuations and one in which loss was strongly density-dependent.

habitable sites and dispersal distance

Dispersal has a particularly important role to play when populations are fragmented and patchy – as many are. The abundance of patchily distributed organisms can be thought of as being determined by the properties of two features: the ‘habitable site’ and the ‘dispersal distance’ (Gadgil, 1971). Thus, a population may be small if its habitable sites are themselves small or short-lived or only few in number; but it may also be small if the dispersal distance between habitable sites is great relative to the dispersibility of the species, such that habitable sites that go extinct locally are unlikely to be recolonized.

To discover the limitations that the accessibility of habitable sites places on abundance, though, it is necessary to identify habitable sites that are not inhabited. This is possible, for example, for a number of butterfly species, because their larvae feed only on one or a few species of patchily distributed plants. Thus, by identifying habitable sites with these plants, whether or not they were inhabited, Thomas et al. (1992) found that the silver-studded blue butterfly *Plebejus argus* was able to colonize virtually all habitable sites less than 1 km from existing populations, but those further away (beyond the dispersal powers of the butterfly) remained uninhabited. The overall size of the population was determined as much by the accessibility of this patchy resource as by the total amount of the resource. Indeed, the habitability of some of these isolated sites was established when the butterfly was successfully introduced there (Thomas & Harrison, 1992). This, after all, is the crucial test of whether an uninhabited ‘habitable’ site is really habitable or not.

metapopulations

A radical change in the way ecologists think about populations has involved combining patchiness and dispersal in the concept of a *metapopulation*, the origins of which are described in Box 9.3. A population can be described as a



## 9.3 HISTORICAL LANDMARKS

### 9.3 Historical landmarks

#### The genesis of metapopulation theory

A classic book, *The Theory of Island Biogeography*, written by MacArthur and Wilson and published in 1967, was an important catalyst in radically changing ecological theory. They showed how the distribution of species on islands could be interpreted as a balance between the opposing forces of extinctions and colonizations (see Chapter 10) and focused attention especially on situations in which those species were all available for repeated colonization of individual islands from a common source – the mainland. They developed their ideas in the context of the floras and faunas of real (i.e. oceanic) islands, but their thinking has been rapidly assimilated into much wider contexts with the realization that patches everywhere have many of the properties of true islands – ponds as islands of water in a sea of land, trees as islands in a sea of grass, and so on.

At about the same time as MacArthur and Wilson's book was published, a simple model of 'metapopulation dynamics' was proposed by Levins (1969). The concept of a *metapopulation* was introduced to refer to a subdivided and patchy population in which the population dynamics operate at two levels:

- 1 The dynamics of individuals within patches (determined by the usual demographic forces of birth, death and movement).
- 2 The dynamics of the occupied patches (or 'subpopulations') themselves within the overall metapopulation (determined by the rates of colonization of empty patches and of extinction within occupied patches).

Although both this and MacArthur and Wilson's theory embraced the idea of patchiness, and both focused on colonization and extinction rather than the details of local dynamics, MacArthur and Wilson's theory was based on a vision of mainlands as rich sources of colonists for whole archipelagos of islands, whereas in a metapopulation there is a collection of patches but no such dominating mainland.

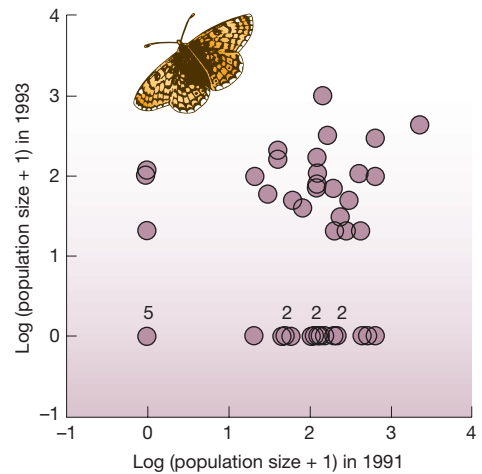
Levins introduced the variable  $p(t)$ , the fraction of habitat patches occupied at time  $t$ . Note that the use of this single variable carries the profound notion that not all habitable patches are always inhabited. The rate of change in  $p(t)$  depends on the rate of local extinction of patches and the rate of colonization of empty patches. It is not necessary to go into the details of Levin's model; suffice to say that as long as the intrinsic rate of colonization exceeds the intrinsic rate of extinction within patches, the total metapopulation will reach a stable, equilibrium fraction of occupied patches, even if none of the local populations is stable in its own right.

Perhaps because of the powerful influence on ecology of MacArthur and Wilson's theory, the whole idea of metapopulations was largely neglected during the 20 years after Levins's initial work. The 1990s, however, saw a great flowering of interest, both in underlying theory and in populations in nature that might conform to the metapopulation concept (Hanski, 1999).

metapopulation if it can be seen to comprise a collection of subpopulations, each one of which has a realistic chance both of going extinct and of appearing again through recolonization. The essence is a change of focus: less emphasis is given to the birth, death and movement processes going on within a single subpopulation; but much more emphasis is given to the colonization (= birth) and extinction (= death) of subpopulations within the metapopulation as a whole. From this

### Figure 9.8

Comparison of the subpopulation sizes in June 1991 (adults) and August 1993 (larvae) of the Glanville fritillary butterfly (*Melitaea cinxia*) on Åland Island in Finland. Multiple data points are indicated by numbers. Many 1991 populations, including many of the largest, had become extinct by 1993.



AFTER HANSKI ET AL., 1995

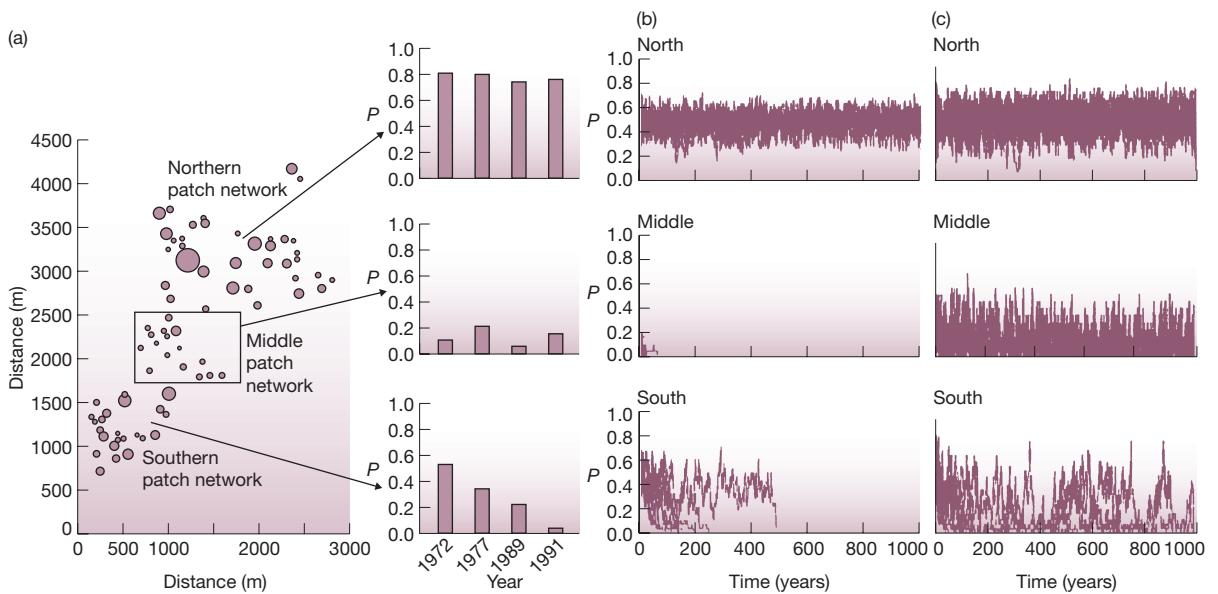
metapopulation dynamics:  
the American pika

perspective, it becomes apparent that a metapopulation may persist, stably, as a result of the balance between extinctions and recolonizations, even though none of the local subpopulations is stable in its own right. An example of this is shown in Figure 9.8, where within a persistent, highly fragmented metapopulation of the Glanville fritillary butterfly (*Melitaea cinxia*) in Finland, even the largest subpopulations had a high probability of declining to extinction within 2 years.

Aspects of the dynamics of metapopulations can be illustrated in a study of a small mammal, the American pika, *Ochotona princeps*, in California (Figure 9.9). The overall metapopulation could itself be divided into northern, middle and southern networks of patches, and the patch occupancy in each was determined on four occasions between 1972 and 1991. These data (Figure 9.9a) show that the northern network maintained a high occupancy throughout the study period, the middle network maintained a more variable and much lower occupancy, while the southern network suffered a steady and substantial decline.

The dynamics of individual subpopulations were not monitored, but these were simulated using models based on the principles of metapopulation dynamics and on general information on pika biology. When the three networks were simulated in isolation (Figure 9.9b), the northern network remained at a stable high occupancy (as observed in the data), but the middle network rapidly and predictably crashed, and the southern network eventually suffered the same fate. However, when the entire metapopulation was simulated as a single entity (Figure 9.9c), the northern network again achieved stable high occupancy, but this time the middle network was also stable, albeit at a much lower occupancy (again as observed), while the southern network suffered periodic collapses (also consistent with the real data).

This all suggests that within the metapopulation as a whole, the northern network acts as a net source of colonizers that prevent the middle network from suffering overall extinction. These in turn delay extinction in, and allow recolonization of, the southern network. The study therefore illustrates how whole metapopulations can be stable when their individual subpopulations are not. Moreover, the comparison of the northern and middle networks, both stable but at very different occupancies, shows how occupancy may depend on the size



**Figure 9.9**

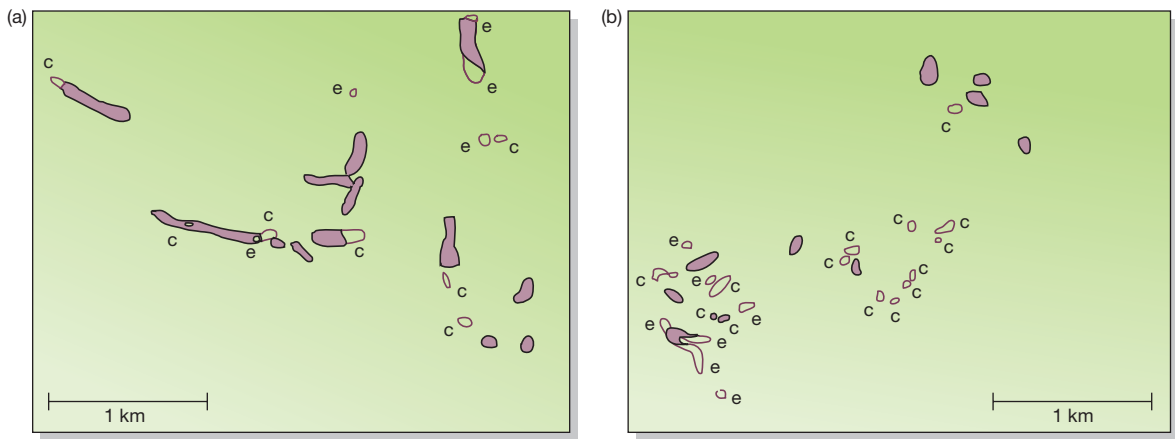
The metapopulation dynamics of the American pika, *Ochotona princeps*, in Bodie, California. (a) The relative positions (distance from a point southwest of the study area) and approximate sizes (as indicated by the size of the dots) of the habitable patches, and the occupancies (as proportions,  $P$ ) in the northern, middle and southern networks of patches in 1972, 1977, 1989 and 1991. (b) The simulated temporal dynamics of the three networks, with each of the networks simulated in isolation. Ten replicate simulations are shown, overlaid on one another, each starting with the actual data in 1972. (c) Equivalent simulations to (b) but with the entire metapopulation treated as a single entity.

of the pool of dispersers, which itself may depend on the size and number of the subpopulations.

Finally, the southern network in particular emphasizes that the observable dynamics of a metapopulation may have more to do with ‘transient’ behavior, far from any equilibrium. To take another example, the silver-spotted skipper butterfly (*Hesperia comma*) declined steadily in Great Britain from a widespread distribution over most calcareous hills in 1900, to 46 or fewer refuge localities (local populations) in 10 regions by the early 1960s (Thomas & Jones, 1993). The probable reasons were changes in land use – increased plowing of grasslands, reduced stocking with grazing animals – and the virtual elimination of rabbits by myxomatosis with its consequent profound vegetational changes. Throughout this non-equilibrium period, rates of local extinction generally exceeded those of recolonization. In the 1970s and 1980s, however, reintroduction of livestock and recovery of the rabbits led to increased grazing, and suitable habitats increased again. This time, recolonization exceeded local extinction, but the spread of the skipper remained slow, especially into localities isolated from the 1960s refuges. Even in southeast England, where the density of refuges was greatest, it is predicted that the abundance of the butterfly will increase only slowly – and remain far from equilibrium – for at least 100 years. Thus, it seems that around a century of ‘transient’ decline in the dynamics of the metapopulation is to be followed by another century of transient increase – except that the environment will no doubt alter again before the transient phase ends and the metapopulation reaches equilibrium.

transient dynamics may be as important as equilibria





**Figure 9.10**

Two metapopulations of the silver-studded blue butterfly (*Plebejus argus*) in North Wales: filled outlines, present in both 1983 and 1990 ('persistent'); open outlines, not present at both times; e, present only in 1983 (presumed extinction); c, present only in 1990 (presumed colonization). (a) In a limestone habitat, where there was a large number of persistent (often larger) local populations among smaller, much more ephemeral local populations (extinctions and colonizations). (b) In a heathland habitat, where the proportion of smaller and ephemeral populations was much greater.

a continuum of  
metapopulation types

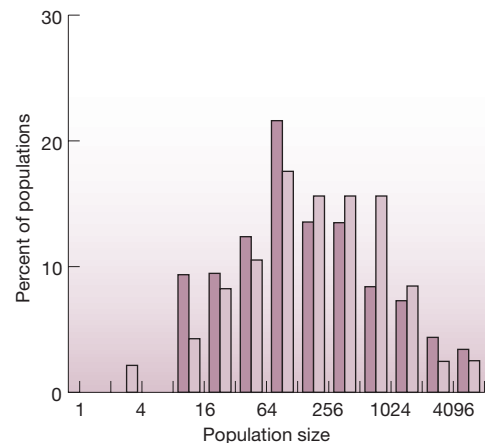
metapopulations of plants?  
remember the seed bank

In reality, moreover, there is likely to be a continuum of types of metapopulation: from collections of nearly identical local populations, all equally prone to extinction, to metapopulations in which there is great inequality between local populations, some of which are effectively stable in their own right. This contrast is illustrated in Figure 9.10 for the silver-studded blue butterfly (*Plebejus argus*) in North Wales, UK.

Finally, we must be wary of assuming that all patchy populations are truly metapopulations – comprising subpopulations, each one of which has a measurable probability of going extinct or being recolonized. The problem of identifying metapopulations is especially apparent for plants. There is no doubt that many plants inhabit patchy environments, and apparent extinctions of local populations may be common. This is shown in Figure 9.11 for the annual aquatic plant *Eichhornia paniculata*, living in temporary ponds and ditches in arid regions

**Figure 9.11**

Of 123 populations of the annual aquatic plant *Eichhornia paniculata* in northeast Brazil observed over a 1-year time interval, 39% went extinct, but the mean initial size of those that went extinct (dark bars) was not significantly different from those that did not (open bars). (Mann-Whitney  $U = 1925$ ,  $P > 0.3$ ).



in northeast Brazil. However, the applicability of the idea of recolonization following a genuine extinction is questionable in any plant species that has a buried seed bank (see Section 5.2.2). In *E. paniculata*, for instance, the heavy seeds almost always drop in the immediate vicinity of the parent rather than being dispersed to other patches. ‘Extinctions’, then, are typically the result of the catastrophic loss of habitat (note in Figure 9.11 that the chance of extinction has effectively nothing to do with the previous population size); and ‘recolonizations’ are almost always simply the result of the germination of seeds following habitat restoration. Recolonization by dispersal, a prerequisite for a true metapopulation, is extremely rare.

## 9.4 Temporal patterns in community composition

### 9.4.1 Founder-controlled and dominance-controlled communities

From the perspective of environmental patchiness, the metapopulation concept is important for our understanding of population dynamics, but when community organization is the focus of attention we usually refer to the *patch dynamics* concept. The concepts are closely related. Both accept that a combination of patchiness and dispersal between patches can give rise to dynamics quite different from those that would be observed if there was just one, homogeneous patch.

Disturbances that open up gaps are common in all kinds of community. Gaps are simply patches within which many species suffer local extinction simultaneously. In forests, high winds, elephants or simply the death of a tree through old age may all create gaps. In grassland, agents include frost, burrowing animals and cattle dung. On rocky shores, gaps may be formed as a result of severe wave action during hurricanes, battering by moored boats or the action of predators.

Two fundamentally different kinds of community organization can be recognized (Yodzis, 1986). When all species are good colonists and essentially equal competitors, communities are described as *founder controlled*; when some species are strongly superior competitively, communities can be described as *dominance controlled*. The dynamics of the two are quite different, and we deal with them in turn.

In founder-controlled communities, species are approximately equivalent in their ability to invade gaps and can hold the gaps against all comers during their lifetime. Hence, the probability of competitive exclusion in the community as a whole may be much reduced where gaps are appearing continually and randomly. This can be referred to as a ‘competitive lottery’. On each occasion that an organism dies (or is killed) a gap is opened for invasion. All conceivable replacements are possible, and species richness is maintained at a high level in the system as a whole. For example, three species of fish co-occur on the upper slope of Heron Reef, part of the Great Barrier Reef off eastern Australia: *Eupomacentrus apicalis*, *Plectroglyphidodon lacrymatus* and *Pomacentrus wardi*. Within rubble patches, the available space is occupied by a series of non-overlapping territories, which individuals hold throughout their juvenile and adult life, defending them against individuals of their own and other species.

disturbances and the patch dynamics concept of community organization

founder-controlled communities: competitive lotteries

The Great Barrier Reef, Australia.



© DAVE FLEETHAM, VISUALS UNLIMITED

But there seems to be no particular tendency for space initially held by one species to be taken up, following mortality, by the same species. Nor is any sequence of ownership evident (Table 9.4). *Pomacentrus wardi* both recruited and lost individuals at a higher rate than the other two species, but all three species appear to have recruited at a sufficient level to balance their rates of loss and maintain a resident population of breeding individuals.

Indeed, communities of tropical reef fish in general may often conform to the founder-controlled model (Sale & Douglas, 1984). They are extremely rich in species. The number of fish species on the Great Barrier Reef ranges from 900 in the south to 1500 in the north, and more than 50 resident species may be recorded on a single patch of reef 3 m in diameter. Only a proportion of this species richness is likely to be attributable to resource partitioning of food and space – indeed the diets of many of the coexisting species are very similar. It is vacant living space that seems to be a crucial limiting factor, generated unpredictably in space and time when a resident dies or is killed. The lifestyles of the species match this state of affairs. They breed often, sometimes year-round, and produce

Table 9.4

For three species of reef fish, the numbers of each species observed occupying sites, or parts of sites, that had been vacated during the immediately prior period between censuses through the loss of residents of each species. The sites vacated through loss of 120 residents were reoccupied by 131 fish; the species of the new occupant is not dependent on the species of the previous resident ( $\chi^2 = 5.88$ ;  $P > 0.1$ ).

RESIDENT LOST	REOCCUPIED BY:		
	<i>E. APICALIS</i>	<i>P. LACRYMATUS</i>	<i>P. WARDI</i>
<i>Eupomacentrus apicalis</i>	9	3	19
<i>Plectroglyphidodon lacrymatus</i>	12	5	9
<i>Pomacentrus wardi</i>	27	18	29

AFTER SALE, 1979

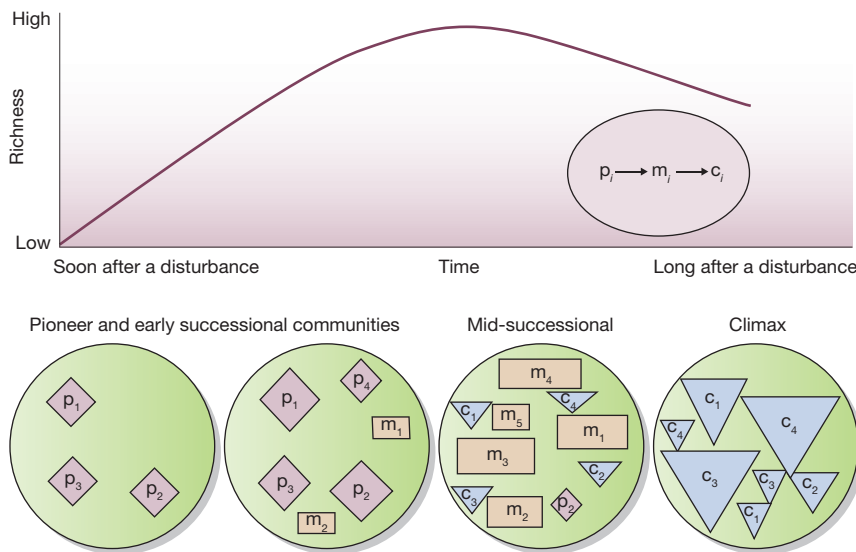


Figure 9.12

Hypothetical succession in a gap – an example of dominance control. The occupancy of gaps is reasonably predictable. Richness begins at a low level as a few pioneer ( $p_i$ ) species arrive; reaches a maximum in midsuccession when a mixture of pioneer, mid-successional ( $m_j$ ) and climax ( $c_i$ ) species occur together; and drops again as competitive exclusion by climax species takes place.

numerous clutches of dispersive eggs or larvae. The species compete in a lottery for living space in which larvae are the tickets, and the first arrival at the vacant space wins the site, matures quickly and holds the space for its lifetime.

In dominance-controlled communities, by contrast, some species are competitively superior to others, and an initial colonizer of a patch cannot necessarily maintain its presence there. In these cases, disturbances that open up gaps lead to reasonably predictable sequences of species, because different species have different strategies for exploiting resources – early species are good colonizers and fast growers, whereas later species can tolerate lower resource levels and grow to maturity in the presence of early species, eventually outcompeting them. Such sequences are examples of community *successions*. An idealized view of a succession is shown in Figure 9.12. Open space is colonized by one or more of a group of opportunistic, early-succession species ( $p_1$ ,  $p_2$ , etc., in Figure 9.12). As time passes, more species invade, often those with poorer powers of dispersal. These eventually reach maturity, dominating mid-succession ( $m_1$ ,  $m_2$ , etc.) and many or all of the pioneer species are driven to extinction. Later still, the community reaches a *climax* stage when the most efficient competitors ( $c_1$ ,  $c_2$ , etc.) oust their neighbors. In this sequence, if it runs its full course, the number of species first increases (because of colonization) then decreases (because of competition).

Some disturbances are synchronized over extensive areas. A forest fire may destroy a huge tract of a climax community. The whole area then proceeds through a more or less synchronous succession. Other disturbances are much smaller and produce a patchwork of habitats. If these disturbances are out of phase with one another, the resulting community comprises a mosaic of patches at different stages of succession.

### 9.4.2 Community succession

If an opened-up gap has not previously been influenced by a community, the sequence of species is referred to as a *primary succession*. Lava flows caused by volcanic eruptions, substrate exposed by the retreat of a glacier and freshly

dominance-controlled  
communities and community  
succession

primary and secondary  
successions

formed sand dunes are all examples. But where the species of an area has been partially or completely removed but seeds and spores remain, the subsequent sequence is termed a *secondary succession*. The loss of trees locally as a result of high winds may lead to secondary successions, as can cultivation followed by the abandonment of farmland (so-called old-field successions).

Primary successions often take several hundreds of years to run their course. However, on recently denuded rocks in the marine subtidal zone a primary succession may take only a decade or so. The research life of an ecologist is sufficient to encompass a subtidal succession but not that following glacial retreat. Fortunately, however, information can sometimes be gained over the longer time scale. Successional stages in time may be represented by community gradients in space. The use of historical maps, carbon dating or other techniques may enable the age of a community since initial exposure to be estimated. A series of communities currently in existence – a ‘chronosequence’ – can then be inferred to reflect succession.

a primary succession in  
duneland

An extensive chronosequence of dune-capped beach ridges occurs on the coast of Lake Michigan in the USA. Thirteen ridges of known age (30–440 years old) show a clear pattern of primary succession to forest. The dune grass *Ammophila breviligulata* dominates the youngest, still mobile, dune ridge. Within 100 years, these are replaced by evergreen shrubs such as *Juniperus communis* and by prairie bunch grass *Schizachyrium scoparium*. Conifers begin colonizing the dune ridges after 150 years, and a mixed forest of pine species develops between 225 and 400 years. Deciduous trees such as the oak and maple do not become important components of the forest until 440 years.

Experimental seed addition and seedling transplants have shown that later species are nonetheless capable of germinating in young dunes (Figure 9.13a). The more developed soil of older dunes may improve the performance of late-successional species, but their successful colonization of young dunes is mainly prevented by limited seed dispersal, together with seed predation by rodents (Figure 9.13b). Eventually, however, the early species are competitively excluded as trees establish and grow.

secondary succession on fields  
abandoned by farmers

Successions on old fields have been studied primarily in the eastern United States, where many farms were abandoned by farmers who moved west after the frontier was opened up in the 19th century. Most of the pre-colonial mixed conifer–hardwood forest had been destroyed, but regeneration was swift after the ‘disturbance’ caused by farmers came to an end. The early pioneers of the American West left behind exposed land that was colonized by pioneers of a very different kind. The typical sequence of dominant vegetation is: annual weeds → herbaceous perennials → shrubs → early successional trees → late successional trees. A particularly detailed study of old-field succession has been performed at the Cedar Creek Natural History Area in Minnesota on well-drained and nutrient-poor soil. This study is discussed in detail in Section 1.3.2.

Old-field succession has also been studied in the productive Loess Plateau in China, which for millennia has been affected by human activities so that few areas of natural vegetation remain. One study examined the vegetation at four plots abandoned by farmers for known periods of time: 3, 26, 46 and 149 years. Of a total of 40 plant species identified, different species were dominant (in terms of relative abundance and relative ground cover) in the different aged plots (Figure 9.14). The early-successional species were annuals and biennials with

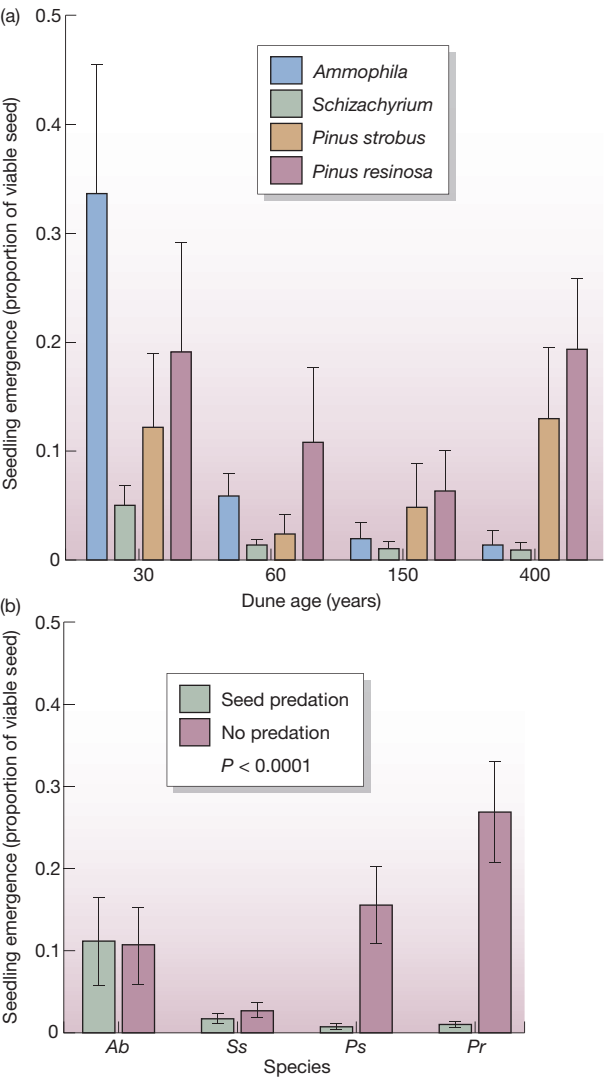


Figure 9.13

(a) Seedling emergence (means + SE) from added seeds of species typical of different successional stages on dunes of four ages. (b) Seedling emergence of the four species (*Ab*, *Ammophila*; *Ss*, *Schizachyrium*; *Ps*, *Pinus strobus*; *Pr*, *Pinus resinosa*) in the presence and absence of rodent predators of seeds.

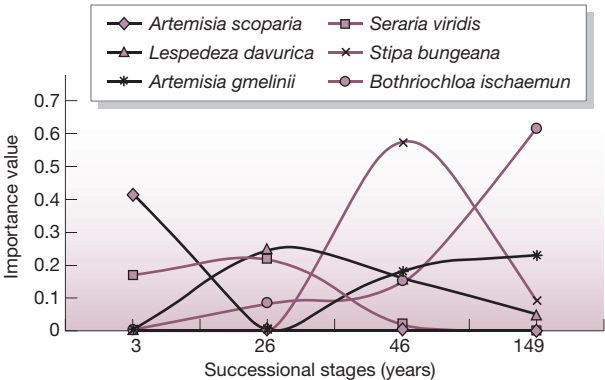


Figure 9.14

Variation in the relative importance of six species during an old-field succession on the Loess Plateau in China.

**Table 9.5**

Some representative photosynthetic rates ( $\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ ) of plants in a successional sequence. Late-successional trees are arranged according to their relative successional position.

PLANT	RATE	PLANT	RATE
<b>Summer annuals</b>		<b>Early-successional trees</b>	
<i>Abutilon theophrasti</i>	24	<i>Diospyros virginiana</i>	17
<i>Amaranthus retroflexus</i>	26	<i>Juniperus virginiana</i>	10
<i>Ambrosia artemisiifolia</i>	35	<i>Populus deltoides</i>	26
<i>Ambrosia trifida</i>	28	<i>Sassafras albidum</i>	11
<i>Chenopodium album</i>	18	<i>Ulmus alata</i>	15
<i>Polygonum pensylvanicum</i>	18		
<i>Setaria faberii</i>	38	<b>Late-successional trees</b>	
<b>Winter annuals</b>		<i>Liriodendron tulipifera</i>	18
<i>Capsella bursa-pastoris</i>	22	<i>Quercus velutina</i>	12
<i>Erigeron annuus</i>	22	<i>Fraxinus americana</i>	9
<i>Erigeron canadensis</i>	20	<i>Quercus alba</i>	4
<i>Lactuca scariola</i>	20	<i>Quercus rubra</i>	7
<b>Herbaceous perennials</b>		<i>Aesculus glabra</i>	8
<i>Aster pilosus</i>	20	<i>Fagus grandifolia</i>	7
		<i>Acer saccharum</i>	6

AFTER BAZZAZ, 1979

high seed production. By 26 years, the perennial herb *Lespedeza davurica*, with its ability to spread laterally by vegetative means and a well-developed root system, had replaced *Artemisia scoparia*. The 46-year-old plot was characterized by the highest species richness and diverse life history strategies, dominated by perennial lifestyles. The dominance of the grass *Bothriochloa ischaemum* at 149 years was related to its perennial nature, ability to spread clonally and high competitive ability. Unlike the abandoned fields of the eastern USA, the climax vegetation of the Loess Plateau appears to be steppe grassland rather than forest. But as in the idealized succession of Figure 9.12, an initial increase in species number as a result of colonization and a subsequent decrease as a result of competition are both apparent.

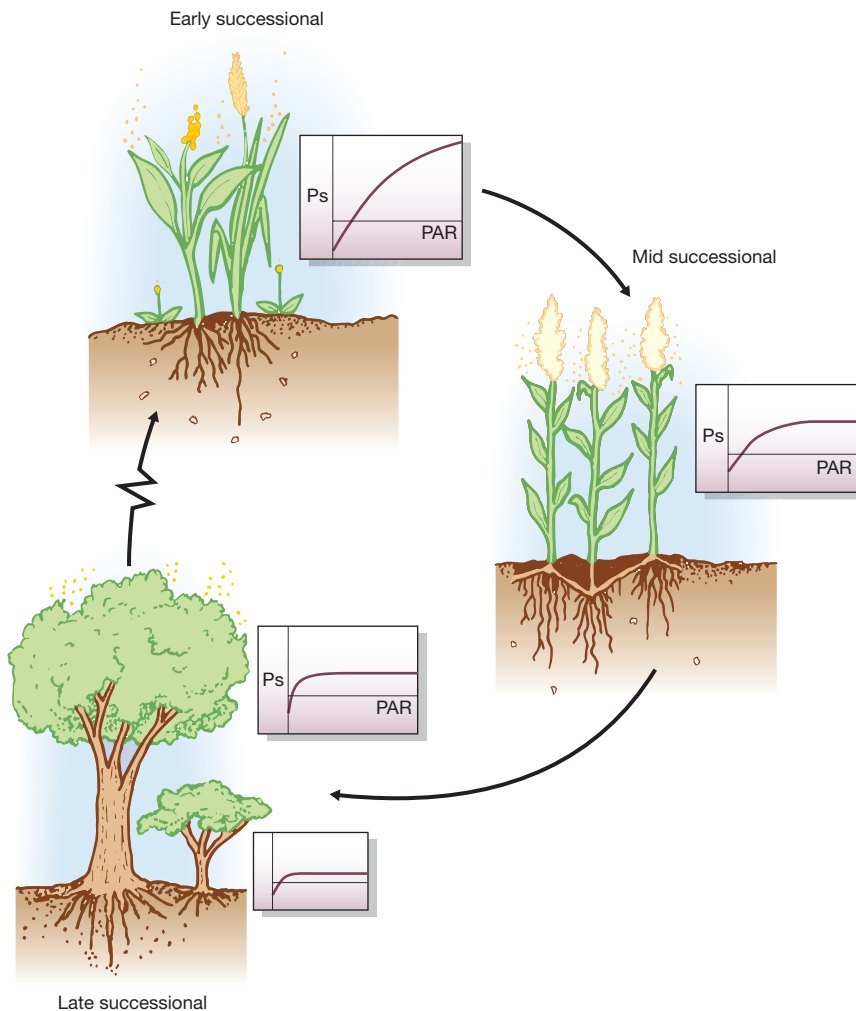
early and late successional  
species have different properties

Early-successional plants have a fugitive lifestyle. Their continued survival depends on dispersal to other disturbed sites. They cannot persist in competition with later species, and thus they must grow and consume the available resources rapidly. High growth and photosynthetic rates are crucial properties of the fugitive. Those of later successional plants are much lower (Table 9.5).

In contrast to the pioneer annuals, seeds of later successional plants can germinate in the shade, for example, beneath a forest canopy. They can continue to grow at these low light intensities, too – quite slowly but faster than the species they replace (Figure 9.15).

The early colonists among the trees usually have efficient seed dispersal; this in itself makes them likely to be early on the scene. They are usually precocious reproducers and are soon ready to leave descendants in new sites elsewhere. The late colonists are those with larger seeds, poorer dispersal and long juvenile phases. The contrast is between the lifestyles of the ‘quickly come, quickly gone’ and ‘what I have, I hold’.



**Figure 9.15**

Idealized light saturation curves (photosynthetic rate,  $P_s$ , plotted against the quantity of photosynthetically active radiation, PAR) for early-, mid-, and late-successional plants.

The fact that plants dominate most of the structure and succession of communities does not mean that the animals always follow the communities that plants dictate. This will often be the case, of course, because the plants provide the starting point for all food webs and determine much of the character of the physical environment in which animals live. But it is also sometimes the animals that determine the nature of the plant community, for example, through heavy grazing or trampling (Box 9.4). More often, though, animals are passive followers of successions among the plants.

Figure 9.12 was described as an idealized succession, and one respect in which it was idealized was in arriving at a climax community at the end. Do real successions reach a climax? Some may. The succession of seaweeds on an overturned boulder may reach a climax in only a few years. Old-field successions, on the other hand, might take 100–300 years to reach a climax, but in that time the probabilities of fire or severe hurricanes, which occur every 70 or so years in New England, are so high that a process of succession may never go to completion. Bearing in

animals are often affected by, but may also affect, plant successions

the concept of a climax community



## 9.4 TOPICAL ECO CONCERNS

### 9.4 Topical ECOncerns

#### Conservation sometimes requires manipulation of a succession

Some endangered animal species are associated with particular stages of a succession. Their conservation then depends on a full understanding of the successional sequence, and intervention may be required to maintain their habitat at an appropriate successional stage.

An intriguing example is provided by a giant New Zealand insect, the weta *Deinacrida mahoeuensis* (Orthoptera, Anostostomatidae). This species, which is believed to have been formerly widespread in forest habitat, was discovered in the 1970s in an isolated patch of gorse (*Ulex europaeus*). Ironically, in New Zealand gorse is an introduced weed that farmers spend much time and effort attempting to control. However, its dense, prickly sward provides a refuge for the giant weta against other introduced pests,

particularly rats but also hedgehogs, stoats and possums, which could readily capture wetas in their original forest home. Mammalian predation is believed to be responsible for weta extinction elsewhere.

New Zealand's Department of Conservation purchased this important patch of gorse from the landowner, who insisted that his cattle should still be permitted to overwinter in the reserve. Conservationists were unhappy about this, but the cattle subsequently proved to be part of the weta's salvation. By opening up paths through the gorse, cattle provided entry for feral goats that browse the gorse, producing a dense hedge-like sward and preventing the habitat from succeeding to a stage inappropriate to the wetas.

This story involves a single, endangered, endemic insect together with a whole suite of introduced pests (gorse, rats, goats, etc.) and introduced domestic animals (cattle). Before the arrival of people in New Zealand, the island's only land mammals were bats, and New Zealand's endemic fauna has proved to be extraordinarily vulnerable to the mammals that arrived with people. However, by maintaining gorse succession at an early stage, the grazing goats provide a habitat in which the wetas can escape the attentions of rats and other predators.



A giant weta on a gorse branch.

COURTESY OF GREG SHERLEY, DEPARTMENT OF CONSERVATION, WELLINGTON, NEW ZEALAND

*Because of its economic cost to farmers, ecologists have been trying to find an appropriate biological control agent for gorse, ideally one that would eradicate it. How would you weigh up the needs of a rare insect against the economic losses associated with gorse on farms?*

successions in a patchwork – the size and shape of gaps

mind that forest communities in northern temperate regions, and probably also in the tropics, are still recovering from the last glaciation, it is questionable whether the idealized climax vegetation is often reached in nature.

In fact, the perception of whether a climax has been reached, like so much else in ecology, is likely to be a matter of scale. As mentioned previously, many successions take place in a mosaic of patches, with each patch, having been

disturbed independently, at a different successional stage. Boulders on a rocky shore are a good example. Climax communities in such cases can then only occur, at best, on a very local scale. Moreover, when successions occur in a patchwork, the nature of the succession, both locally and overall, is likely to depend on the size and shape of the patches (gaps). The centers of very large gaps are most likely to be colonized by species producing propagules that travel relatively great distances. Such mobility is less important in small gaps, since most recolonization will be by propagules from, or simply lateral movement by, established individuals around the periphery.

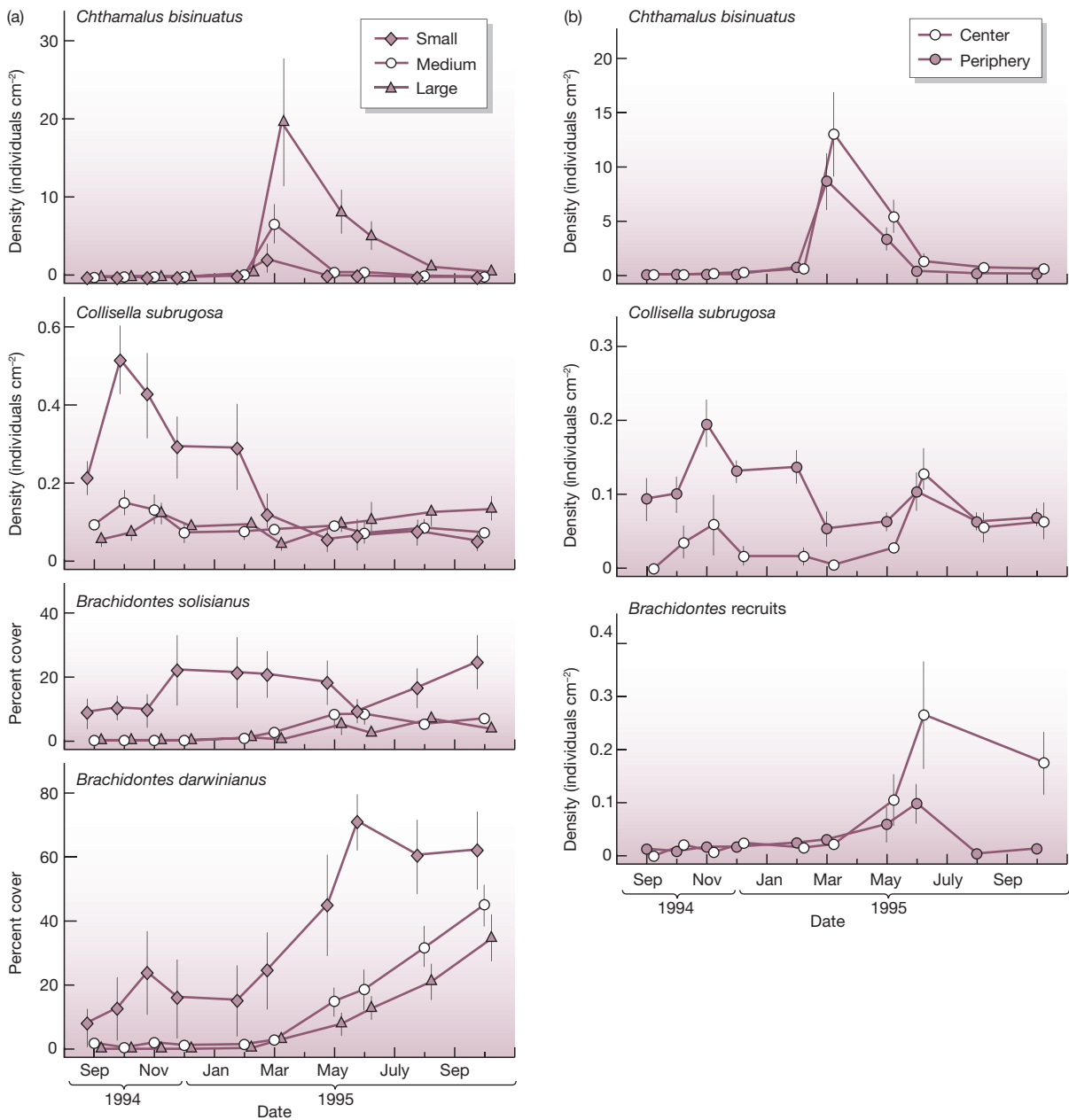
Intertidal beds of mussels provide excellent opportunities to study the processes of formation and filling-in of gaps. In the absence of disturbance, mussel beds may persist as extensive monocultures. More often, they are an ever-changing mosaic of many species that inhabit gaps formed by the action of waves. The size of these gaps at the time of formation ranges from a single mussel space to hundreds of square meters. Gaps begin to fill as soon as they are formed. An experimental study of mussel beds of *Brachidontes solisianus* and *B. darwinianus* in Brazil aimed to determine the effects of patch size and location within a patch on the dynamics of succession (Figure 9.16).

High densities of the limpet *Collisella subrugosa* occurred in the smallest gaps in the first 6 months after gap formation, but not in medium or large gaps (Figure 9.16a). It was also much quicker to colonize the periphery than the center of the large gaps (Figure 9.16b). This association of the limpets with patch edges (and hence small patches) probably occurs because they are less vulnerable there to visually hunting predators. Small gaps were also most quickly colonized by lateral migration of the two mussel species (Figure 9.16a), but from around 6 months, *B. darwinianus* increasingly predominated and also built up its numbers in the medium and large gaps. In the absence of further disturbance, *B. darwinianus* would seem likely to outcompete *B. solisianus*. After around 6 months, too, the *Brachidontes* mussels, which cannot be identified to species when they are small, recruited significantly from settled larvae in the central areas of the large gaps (Figure 9.16b). Finally, the barnacle *Chthamalus bisinuatus* also recruited from settled larvae, largely as a pulse after around 6 months, especially in the largest gaps (Figure 9.16a) and more in the center than at the periphery of the large gaps (Figure 9.16b).

Thus, the smaller the gap, the more the succession within it was dominated by lateral movement than by true migration, and even within a large gap, succession proceeded differently at the center and at the periphery. On the shore as a whole, as in any patchy and disturbed habitat, there was a mosaic of patches in different successional states – those states being determined by patch size, the time since the last disturbance and even on location within a patch.

## 9.5 Food webs

No predator–prey, parasite–host or grazer–plant pair exists in isolation. Each is part of a complex web of interactions with other predators, parasites, food sources and competitors within its community. Ultimately, it is these food webs that ecologists wish to understand. However, it has been useful to isolate groups of competitors as we did in Chapter 6, of predator–prey and parasite–host pairs as in Chapter 7,



**Figure 9.16**

(a) Mean abundances (± SE) of four colonizing species in experimentally cleared small, medium and large gaps in intertidal mussel beds.  
 (b) Recruitment of three species at the periphery (within 5 cm of the gap edge) and in the centre of 400 cm² square gaps.

and of mutualists as in Chapter 8, simply because we have little or no hope of understanding the whole unless we have some understanding of the component parts. Toward the end of Chapter 7 (Section 7.6), our field of view was expanded to include the effects of predators on groups of competitors and to show, for example, the importance of predator-mediated coexistence.

We now take this approach a stage further to focus on systems with at least three trophic levels (plant–herbivore–predator), and consider not only direct but also indirect effects that a species may have on others on the same or other trophic levels. The effects of a predator on individuals or even populations of its herbivorous prey, for example, are direct and relatively straightforward. But these effects may also be felt by any plant population on which the herbivore feeds, or by other predators of the herbivore, or other consumers of the plant, or competitors of the herbivore, or by the myriad species linked even more remotely in the food web.

food webs – shifting the focus to systems with at least three trophic levels

### 9.5.1 Indirect and direct effects

The deliberate removal of a species from a community can be a powerful tool in unraveling the workings of a food web. We might expect such removal to lead to an increase in the abundance of a competitor, or, if the species removed is a predator, to an increase in the abundance of its prey. Sometimes, however, when a species is removed, a competitor may actually decrease in abundance, and the removal of a predator can lead to a decrease in a prey population. Such unexpected effects arise when direct effects are less important than effects that occur through indirect pathways. For example, removal of a species might increase the density of one competitor, which in turn causes another competitor to decline.

These indirect effects are brought especially into focus when the initial removal is carried out for some managerial reason, since the deliberate aim is to solve a problem, not create further, unexpected problems. For example, there are many islands on which feral cats have been allowed to escape domestication and now threaten native prey, especially birds, with extinction. The ‘obvious’ response is to eliminate the cats (and conserve their island prey), but as a simple model shows (Figure 9.17), the programs may not have the desired effect, especially where, as is often the case, rats have also been allowed to colonize the island. The rats typically both compete with and prey upon the birds. The cats normally prey upon the rats as well as the birds. Hence, removal of the cats will relieve the pressure on the rats and is thus likely to increase not decrease the threat to the birds. For example, introduced cats on Stewart Island, New Zealand preyed upon an endangered flightless parrot, the kakapo, *Strigops habroptilus* (Karl & Best, 1982). But controlling cats alone would have been risky, since their preferred prey are three species of introduced rats, which, unchecked, could pose far more of a threat to the kakapo. In fact, Stewart Island’s kakapo population was translocated to smaller offshore islands where exotic predators (like rats) were absent.

cats, rats and birds

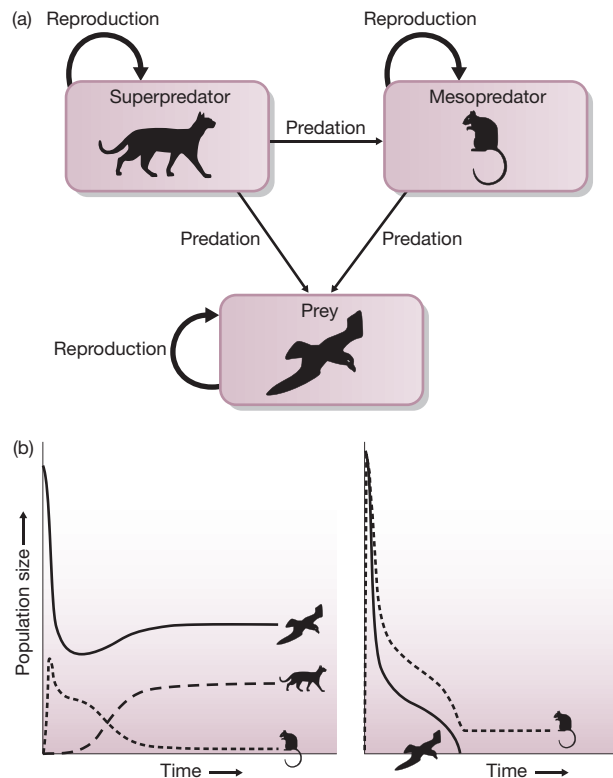
The indirect effect within a food web that has probably received most attention is the so-called *trophic cascade*. It occurs when a predator reduces the abundance of its prey, and this cascades down to the trophic level below, such that the prey’s own resources (typically plants) increase in abundance. Of course, it need not stop there. In a food chain with four links, a top predator may reduce the abundance of an intermediate predator, which may allow the abundance of a herbivore to increase, leading to a decrease in plant abundance.

trophic cascades – effects of shorebirds on limpet populations

One example of a trophic cascade, but also of the complexity of indirect effects, is provided by a 2-year experiment in which predation by birds was experimentally manipulated in an intertidal community on the northwest coast of the United States to determine the consequences for three limpet species and their algal food. Glaucous-winged gulls (*Larus glaucescens*) and oystercatchers

**Figure 9.17**

(a) Schematic representation of a model of an interaction in which a superpredator (such as a cat) preys both on mesopredators (such as rats, for which it shows a preference) and on prey (such as birds), while the mesopredator also attacks the prey. Each species also recruits to its own population, 'reproduction'. (b) The output of the model with realistic values for rates of predation and reproduction: with all three species present, the superpredator keeps the mesopredator in check and all three species coexist (left); but in the absence of the superpredator, the mesopredator drives the prey to extinction (right).

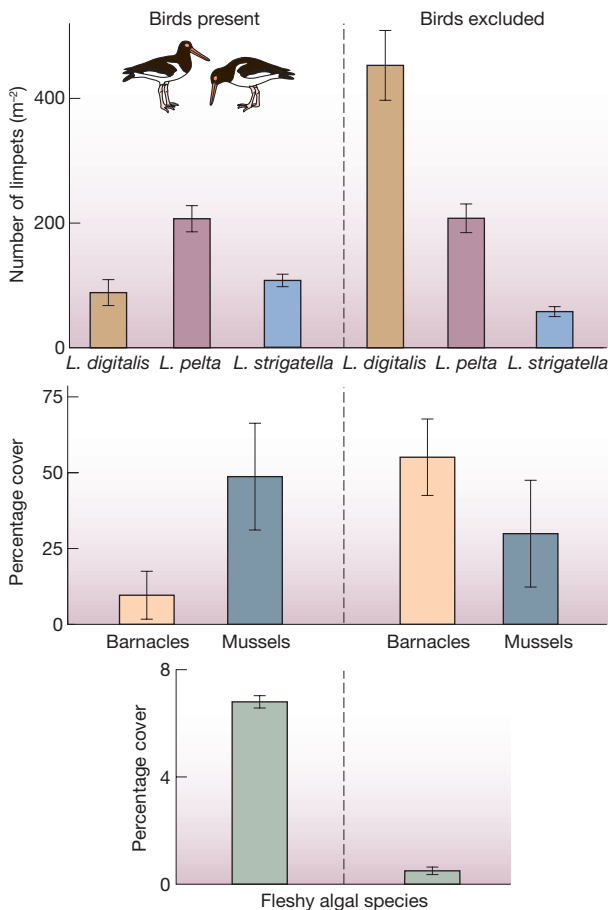


AFTER COURCHAMP ET AL., 1999

(*Haematopus bachmani*) were excluded by means of wire cages from large areas (each 10 m<sup>2</sup>) in which limpets were common. It became evident that excluding the birds increased the overall abundance of one of the limpet species, *Lottia digitalis*, as might have been expected, but a second limpet species (*L. strigatella*) became rarer, and the third, *L. pelta*, which was the one most frequently consumed by the birds, did not vary in abundance. The reasons are complex and go well beyond the direct effects of birds eating limpets (Figure 9.18).

*L. digitalis*, a light-colored limpet, tends to occur on light-colored goose barnacles (*Pollicipes polymerus*) where it is camouflaged, whereas the dark *L. pelta* occurs primarily on dark Californian mussels (*Mytilus californianus*). Predation by birds normally reduces the area covered by goose barnacles, and so excluding the birds increased goose barnacle abundance and also increased the abundance of *L. digitalis* (Figure 9.18). Increasing barnacle abundance also led to a decrease in the area covered by mussels, because they were now subject to more intense competition from the barnacles. This, one imagines, might have led to a decrease in the abundance of *L. pelta*, living predominantly on those mussels. However, the third limpet species, *L. strigatella*, is competitively inferior to the others, and the increase in abundance of *L. digitalis* therefore led to a decrease in the abundance of *L. strigatella*, which in turn released pressure on *L. pelta* such that overall its abundance remained effectively unchanged.

But the effects of bird predation also cascade down to the plant trophic level, because by consuming limpets, the birds normally reduce the grazing pressure of the limpets on fleshy algae, and by consuming goose barnacles, the birds

**Figure 9.18**

When birds are excluded from the intertidal community, barnacles increase in abundance at the expense of mussels, and three limpet species show marked changes in density, reflecting changes in the availability of cryptic habitat and competitive interactions as well as the easing of direct predation. Algal cover is much reduced in the absence of effects of birds on intertidal animals (means and standard errors are shown).

normally free up space for algal colonization. Hence, when the birds were excluded, algal cover decreased (Figure 9.18).

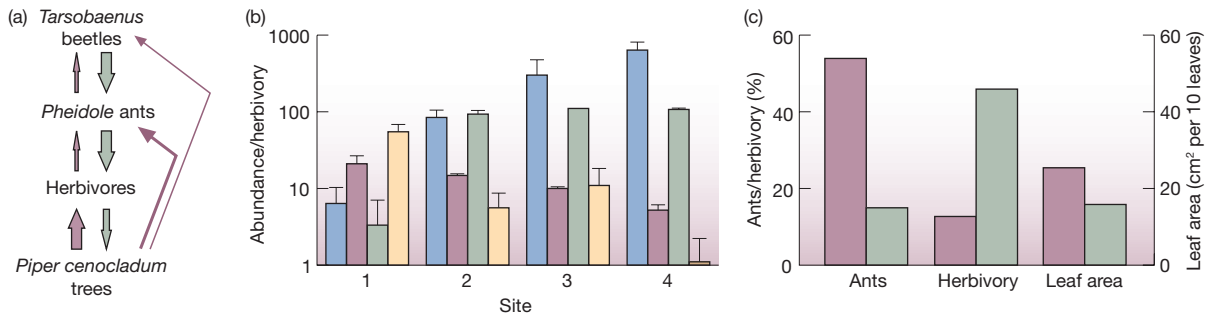
In a four-trophic-level system, if it is subject to trophic cascade, we might expect that as the abundance of a top carnivore increases, the abundances of primary carnivores in the trophic level below decrease, those of the herbivores therefore increase, and plant abundance decreases. This is what was found in a study, in the tropical lowland forests of Costa Rica, of *Tarsobaenus* beetles preying on *Pheidole* ants that prey on a variety of herbivores that attack ant-plants, *Piper cenocladum* (Figure 9.19a). These showed precisely the alternation of abundances expected in a four-trophic-level cascade: relatively high abundances of plants and ants associated with low levels of herbivory and beetle abundance at three sites, but low abundances of plants and ants associated with high levels of herbivory and beetle abundance at a fourth (Figure 9.19b). Moreover, when beetle abundance was manipulated experimentally at one of the sites, ant and plant abundance were significantly higher, and levels of herbivory lower, in the absence of beetles than in their presence (Figure 9.19c).

However, in another four-trophic-level community, in the Bahamas, consisting of sea grape shrubs, which were fed upon by herbivorous arthropods, and then web spiders (primary carnivores) and lizards (top carnivores), the results of

four trophic levels . . .

. . . that can act like three





**Figure 9.19**

(a) Schematic representation of a four-level food chain in Costa Rica. Green arrows denote mortality and maroon arrows a contribution to the consumer's biomass; arrow breadth denotes their relative importance. Both (b) and (c) show evidence of a trophic cascade flowing down from the beetles: positive correlations between beetles and herbivores and between ants and trees. (b) At four sites, the relative abundance of ant-plants (blue bars), the abundance of beetles (maroon bars) and of ants (green bars) and the strength of herbivory (yellow bars) are shown. Means and standard errors are shown; the units of measurement are various and are given in the original references. (c) The results of an experiment at site 4 when replicate enclosures were established without beetles (maroon bars) and with beetles (green bars).

AFTER LETOURNEAU & DYER, 1998A, 1998B; PACE ET AL., 1999

experimental manipulations indicated a strong direct effect of the lizards on the herbivores but a weaker effect of the lizards on the spiders. Consequently, the net effect of top predators on plants was positive and there was less leaf damage in the presence of lizards. In essence, this four-trophic-level community functions as if it has only three levels.

We have seen that trophic cascades are normally viewed 'from the top', starting at the highest trophic level. So, in a three-trophic-level community, we think of the predators controlling the abundance of the herbivores and exerting top-down control. Reciprocally, the predators are subject to bottom-up control: abundance determined by their resources. The plants are also subject to bottom-up control, having been released from top-down control by the effects of the predators on the herbivores. Thus, in a trophic cascade, top-down and bottom-up controls alternate as we move from one trophic level to the next.

But suppose instead that we start at the other end of the food chain, and assume that the plants are controlled bottom-up by competition for their resources. It is still possible for the herbivores to be limited by competition for plants – *their* resources – and for the predators to be limited by competition for herbivores. In this scenario, all trophic levels are subject to bottom-up control, because the resource controls the abundance of the consumer but the consumer does not control the abundance of the resource. The question therefore arises: 'Are food webs – or are particular *types* of food web – dominated by either top-down or bottom-up control?'

The widespread importance of top-down control, foreshadowing the idea of the trophic cascade, was first advocated in a famous paper by Hairston et al. (1960), which asked 'Why is the world green?' They answered, in effect, that the world is green because top-down control predominates: green plant biomass accumulates because predators keep herbivores in check.

Murdoch (1966), in particular, challenged these ideas. His view, described by Pimm (1991) as 'the world is prickly and tastes bad', emphasized that even if the world is green (assuming it is), it does not necessarily follow that the herbivores are failing to capitalize on this because they are limited, top down, by their predators.

top-down or bottom-up control of food webs?

why is the world green? . . .

. . . or is it prickly and bad tasting?

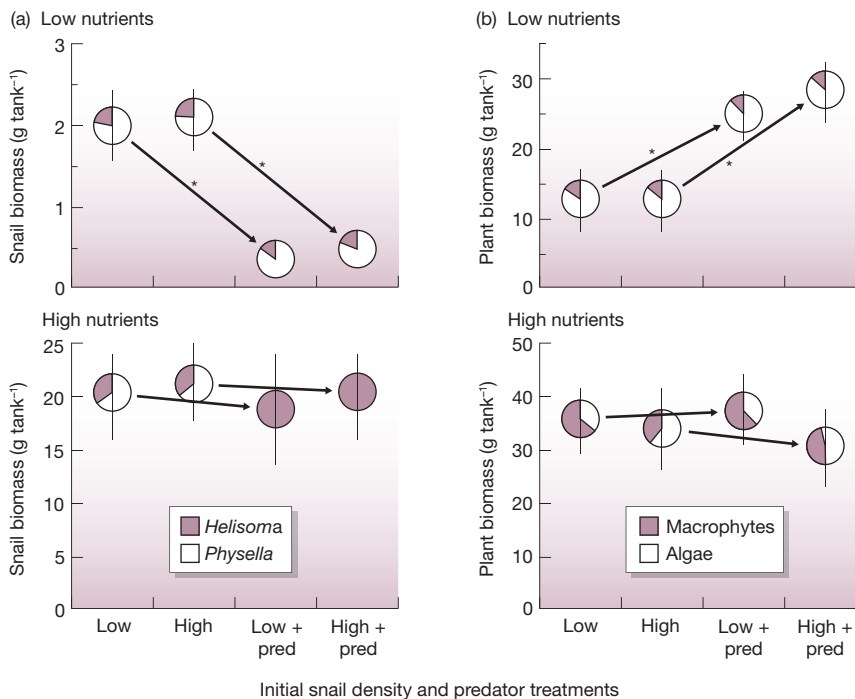


Figure 9.20

Top-down control, but only with low productivity. (a) Snail biomass and (b) plant biomass in experimental ponds with low or high nutrient treatments (vertical bars are standard errors). With low nutrients, the snails were dominated by the insect predator *Physella* (vulnerable to predation) and the addition of predators led to a significant decline (indicated by \*) in snail biomass and a consequent increase in plant biomass (dominated by algae). But with high nutrients, *Helisoma* snails (less vulnerable to predation) increased their relative abundance, and the addition of predators led neither to a decline in snail biomass nor an increase in plant biomass (often dominated by macrophytes).

Many plants have evolved physical and chemical defenses that make life difficult for herbivores. The herbivores may therefore be competing fiercely for a limited amount of palatable and unprotected plant material; and their predators may, in turn, compete for scarce herbivores. A world controlled from the bottom up may still be green.

That very little is required to switch control from one type to the other is emphasized by a study that examined the effect of nutrient concentrations on a freshwater web comprising an insect predator (*Physella gyrina*) feeding on two species of herbivorous snails feeding on water plants and algae (Figure 9.20). At the lowest nutrient concentrations, the snails were dominated by the smaller *P. gyrina* (they were vulnerable to predation), and the predator gave rise to a trophic cascade extending to the plants and algae. But at the highest nutrient concentrations, the snails were dominated by the larger *Helisoma trivolvis* (they were relatively invulnerable to predation), and no trophic cascade was apparent. This study, therefore, also lends support to Murdoch's proposition that 'the world tastes bad', in that invulnerable herbivores gave rise to a web with a relative dominance of bottom-up control. Overall, though, the elucidation of clear patterns in the predominance of top-down or bottom-up control remains a challenge for the future.

### 9.5.2 Population and community stability and food web structure

Of all the imaginable food webs in nature, are there particular types that we tend to observe repeatedly? Are some food web structures more stable than others? (We discuss what *stable* means in Box 9.5.) Do we observe particular types of



## 9.5 Quantitative aspects

### 9.5 QUANTITATIVE ASPECTS

#### What do we mean by 'stability'?

Among several, there are two important qualifications that can be made when we come to decide what we mean by stability. The first is the distinction between the resilience of a community and its resistance. A *resilient community* is one that returns rapidly to something like its former structure after that structure has been altered. A *resistant community* is one that undergoes relatively little change in its structure in the face of a disturbance.

The second distinction is between *fragile* and *robust stability*. A community has only fragile stability if it remains essentially unchanged in the face of a small disturbance but alters utterly when subjected to a larger disturbance, whereas one that stays roughly the same in the face of much larger disturbances is said to have stability that is dynamically robust.

To illustrate these distinctions by analogy, consider the following:

- a pool or billiard ball balanced carefully on the end of a cue

- the same ball resting on the table
- the ball sitting snugly in its pocket

The ball on the cue is stable in the narrow sense that it will stay there forever as long as it is not disturbed – but its stability is fragile, and both its resistance and its resilience are low: the slightest touch will send the ball to the ground, far from its former state (low resistance), and it has not the slightest tendency to return to its former position (low resilience).

The same ball resting on the table has a similar resilience: it has no tendency to return to exactly its former state (assuming the table is level), but its resistance is far higher: pushing or hitting it moves it relatively little. And its stability is also relatively robust: it remains 'a ball on the table' in the face of all sorts and all strengths of assault with the cue.

The ball in the pocket, finally, is not only resistant but resilient too – it moves little and then returns – and its stability is highly robust: it will remain where it is in the face of almost everything other than a hand that carefully plucks it away.

food web *because* they are stable (and hence persist)? Are populations themselves more stable when embedded in some types of food web than in others? These are important practical questions. We require answers if we are to determine whether some communities are more fragile (and more in need of conservation) than others; or whether there are certain 'natural' structures that we should aim for when we construct communities ourselves; or whether communities that have been restored are likely to stay 'restored'.

'Stability', of course, means stability in the face of a disturbance or perturbation, and most disturbances are, in practice, the loss of one or more populations from a community. What are the knock-on effects of such a loss? How profound are the consequences of the loss of that population for the rest of the community? Some species are more intimately and tightly woven into the fabric of a food web than others. A species whose removal would produce a significant effect (extinction or a large change in density) in at least one other species may be thought of as a strong interactor. The removal of some strong interactors leads to significant changes spreading throughout the food web – we refer to these as *keystone species*.

keystones in food web  
architecture

In building construction, a keystone is the wedge-shaped block at the highest point of an arch that locks the other pieces together. The removal of the keystone species, just like removal of the keystone in an arch, leads to collapse of the structure: it leads to extinction or large changes in abundance of several species, producing a community with a very different species composition. A more precise definition of a keystone species is one whose impact is ‘disproportionately large relative to its abundance’ (Power et al., 1996). This has the advantage of excluding from keystone status what would otherwise be rather trivial examples, especially species at lower trophic levels that may provide the resource on which a whole myriad of other species depend – for example, a coral, or the oak trees in an oak woodland.

Although the term was originally applied only to predators, it is now widely accepted that keystone species can occur at any trophic level. For example, lesser snow geese (*Chen caerulescens caerulescens*) are herbivores that breed in large colonies in coastal marshes along the west coast of Hudson Bay in Canada. At their nesting sites in spring, before growth of above-ground foliage begins, adult geese grub for the roots and rhizomes of plants in dry areas and eat the swollen bases of shoots of sedges in wet areas. Their activity creates bare areas (1–5 m<sup>2</sup>) of peat and sediment. Few pioneer plant species are able to recolonize these patches, and recovery is very slow. Furthermore, in areas of intense summer grazing, ‘lawns’ of *Carex* and *Puccinellia* spp. have become established. Here, therefore, high densities of grazing geese are essential to maintain the species composition of the vegetation and its above-ground production (Kerbes et al., 1990). The lesser snow goose is a keystone species – the whole structure and composition of these communities are drastically altered by its presence.

For a long time, the conventional wisdom, arrived at largely through ‘logical’ argument, was that increased complexity within a community leads to increased stability (MacArthur, 1955; Elton, 1958); that is, more complex communities are more stable in the face of a disturbance such as the loss of one or more species. For example, it was argued that in more complex communities, with more species and more interactions, there were more possible pathways by which energy passed through the community. Hence, if there was a perturbation to the community (a change in the density of one of the species), this would affect only a small proportion of the energy pathways and would have relatively little effect on the densities of other species: the complex community would be resistant to change (Box 9.5).

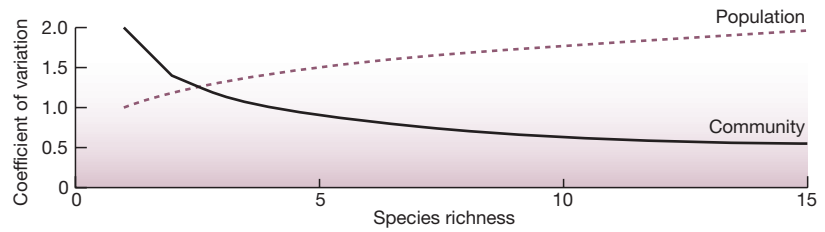
However, as analyses of mathematical models of food webs have become more sophisticated, the conventional wisdom has by no means always received support (May, 1981; Tilman, 1999), and conclusions differ depending on whether we focus on individual populations within a community or on aggregate properties of the community such as their biomass or productivity. Briefly, the model food webs have been characterized by one or more of the following: (i) the number of species they contain; (ii) the *connectance* of the web (the fraction of all possible pairs of species that interact directly with one another); and (iii) the average interaction strength between pairs of species. At the level of the individual population, models have not always come to the same conclusion, but overall they suggest that increases in the number of species, increases in connectance and increases in average interaction strength – each representing an increase in complexity – all tend to *decrease* the tendency of individual populations within the community to return to their former state following a disturbance (their resilience, e.g. Figure 9.21). Thus these models suggest, if anything, that community complexity leads to population *instability*.

a long-standing belief that complexity leads to stability . . .

. . . that is not supported by mathematical models for individual populations

**Figure 9.21**

The effect of species richness (number of species) on the temporal variability (coefficient of variation, CV) of population size and aggregate community abundance in model communities in which all species are equally abundant and have the same CV. Thus, high values for CV equate to low levels of stability.



but aggregate properties are more stable in richer model communities

complexity and stability in practice: populations

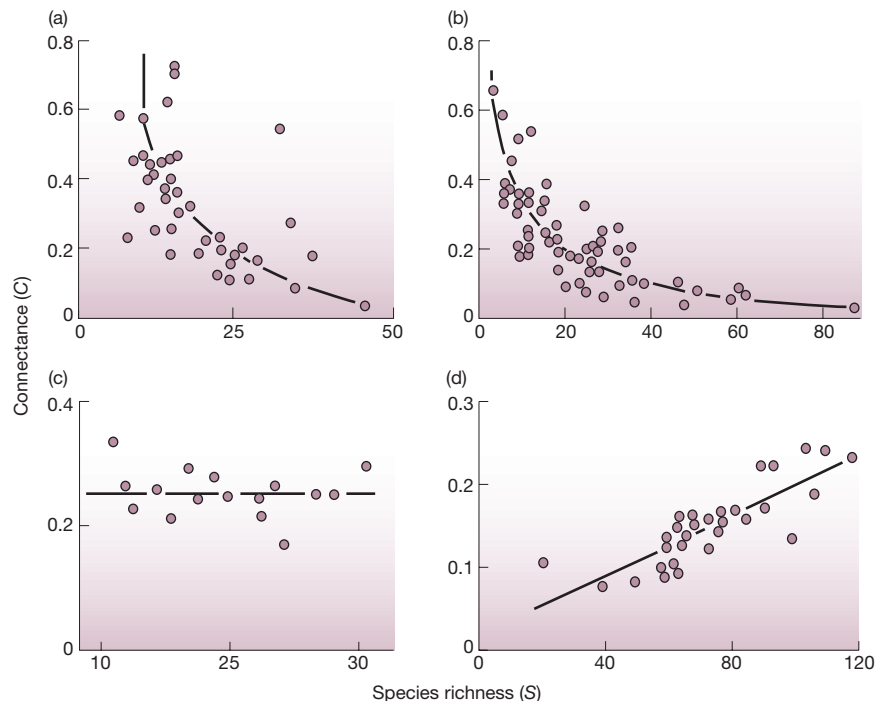
However, the effects of complexity, especially species richness, on the stability of aggregate properties of model communities have been more consistent. Broadly, in richer communities, the dynamics of these aggregate properties are *more* stable (Figure 9.22). In large part, this is because, as long as the fluctuations in different populations are not perfectly correlated, there is an inevitable ‘statistical averaging’ effect when populations are added together – when one goes up, another is going down – and this tends to increase in effectiveness as richness (the number of populations) increases. Certainly, models indicate that there is no necessary, unavoidable connection linking stability to complexity.

What is the evidence from real communities? Various studies have sought to build on the mathematical models by examining the relationships among number of species, connectance and interaction strength. The argument runs as follows. The only communities we can observe are those that are stable enough to exist. Hence, those with more species can only be sufficiently stable if there are compensatory decreases in connectance and/or interaction strength. But data on interaction strengths for whole communities are unavailable, so we assume, for simplicity, that average interaction strength is constant. Thus, communities with more species will only retain stability if there is an associated reduction in average connectance.

**Figure 9.22**

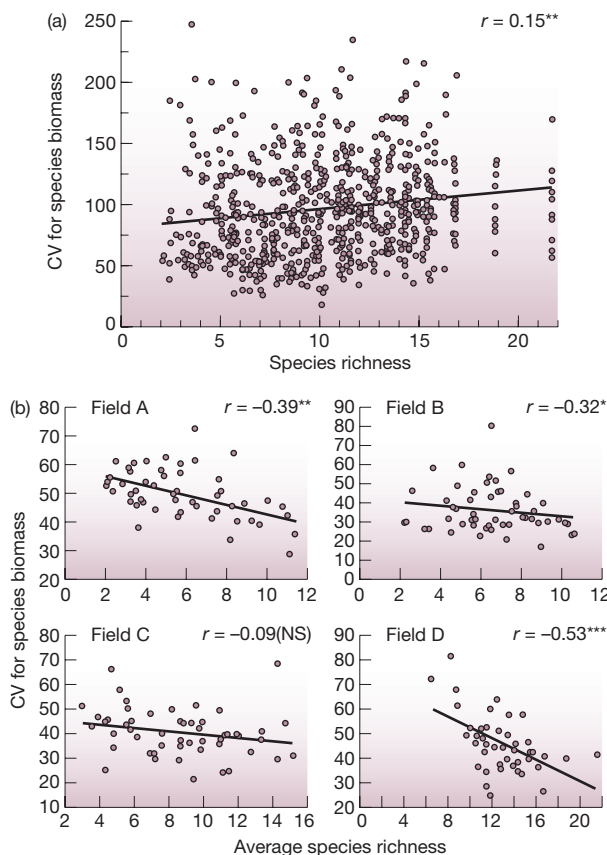
The relationships between connectance and species richness. (a) A compilation from the literature of 40 food webs from terrestrial, freshwater and marine environments. (b) A compilation of 95 insect-dominated webs from various habitats. (c) Seasonal versions of a food web for a large pond in northern England, varying in species richness from 12 to 32. (d) Food webs from swamps and streams in Costa Rica and Venezuela.

(a) AFTER BRIAND, 1983; (b) FROM SCHOENLY ET AL., 1991; (c) FROM WARREN, 1989; (d) FROM WINEMILLER, 1990; AFTER HALL & RAFFAELLI, 1993



Early analyses of published food web data found, as predicted, that connectance decreased with species number (Figure 9.22a). These data, however, were not collected for the purpose of quantitative study of food web properties. In particular, the accuracy of identification varied substantially from web to web, and even in the same web components were sometimes grouped at the level of kingdom (e.g. 'plants'), sometimes as a family (e.g. Diptera) and sometimes as a species (polar bear) (see review by Hall & Raffaelli, 1993). More recent studies, in which food webs were more rigorously documented, indicate that connectance may decrease with species number (as predicted) (Figure 9.22b), or may be independent of species number (Figure 9.22c), or may even increase with species number (Figure 9.22d). Thus, the stability argument does not receive consistent support from food web analyses either.

The prediction that populations in richer communities are less stable when disturbed was also investigated by Tilman (1996), who pooled data for 39 common plant species from 207 grassland plots in Cedar Creek Natural History Area, Minnesota, collected over an 11-year period. He found that variation in the biomass of individual species increased significantly, but only very weakly, with the richness of the plots (Figure 9.23a). Thus, like the theoretical studies, empirical studies hint at decreased population stability (increased variability) in more complex communities, but the effect seems to be weak and inconsistent.

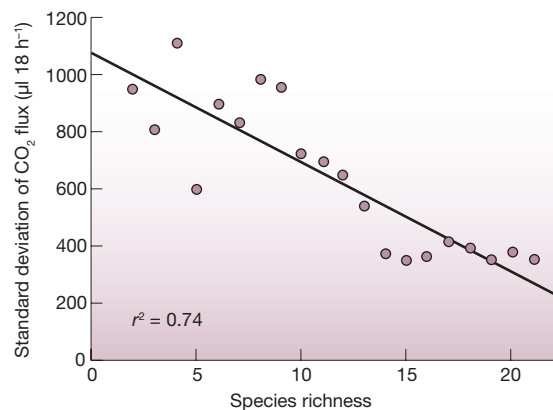


**Figure 9.23**

(a) The coefficient of variation (CV) of population biomass for 39 plant species from plots in four fields in Minnesota over 11 years (1984–1994) plotted against species richness in the plots. Variation increased with richness but the slope was very shallow. (b) The CV for community biomass in each plot plotted against species richness for each of the four fields (A–D). Variation consistently decreased with richness. In both cases, regression lines and correlation coefficients are shown (\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ).

**Figure 9.24**

Variation (i.e. 'instability') in productivity (standard deviation of carbon dioxide flux) declined with species richness in microbial communities observed over a 6-week period.



AFTER MCGRADY-STEED ET AL., 1997

complexity and stability in practice: whole communities

importance of the nature of the community: keystones again

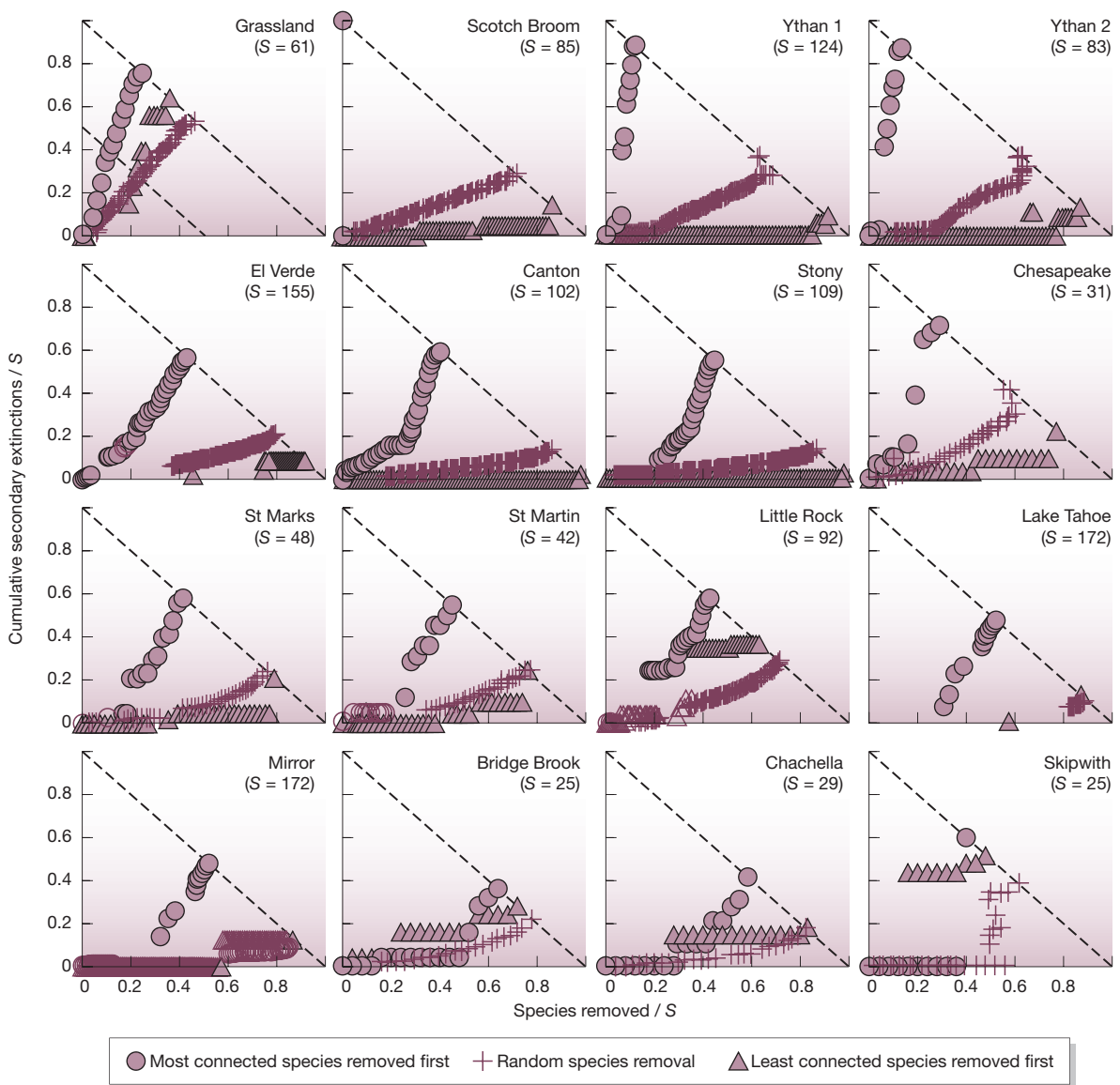
environmental predictability linked to community fragility?

Turning to the aggregate, whole-community level, evidence is largely consistent in supporting the prediction that increased richness in a community increases stability (decreases variability). For example, in Tilman's (1996) Minnesota grasslands study, in contrast to the weak negative effect found at the population level, there was a strong positive effect of richness on the stability of community biomass (Figure 9.23b). Also, McGrady-Steed et al. (1997) manipulated richness in aquatic microbial communities (producers, herbivores, bacterivores, predators) and found that variation in another community measure, carbon dioxide flux (a measure of community respiration), also declined with richness (Figure 9.24).

On the other hand, in an experimental study of small grassland communities perturbed by an induced drought, Wardle et al. (2000) found detailed community composition to be a far better predictor of stability than overall richness. Indeed, it is clear that the whole concept of a keystone species (see above) is itself a recognition of the fact that the effects of a disturbance on structure or function are likely to depend very much on the precise nature of the disturbance – that is, on *which* species are lost. Reinforcement of this idea is provided by a simulation study carried out by Dunne et al. (2002), in which they took 16 published food webs and subjected them to the sequential removal of species. Secondary extinctions followed most rapidly when the most connected species were removed, and least rapidly when the least connected were removed, with random removals lying between the two (Figure 9.25). This reminds us that the idiosyncrasies of individual webs are likely always to undermine the generality of any 'rules' even if such rules can be agreed on.

In fact, even if complexity and instability are connected in models, this does not necessarily mean that we should expect to see an association between complexity and instability in real communities. Unstable communities will fail to persist when they experience environmental conditions that reveal their instability. But the range and predictability of environmental conditions will vary from place to place. In a stable and predictable environment, a community that is dynamically fragile may nevertheless persist. But in a variable and unpredictable environment, only a community that is dynamically robust will be able to persist. Hence, we might expect to see: (i) complex and fragile communities in stable and predictable environments, with simple and robust communities in variable and unpredictable environments; but (ii) approximately the same *observed* stability (in terms of population fluctuations,





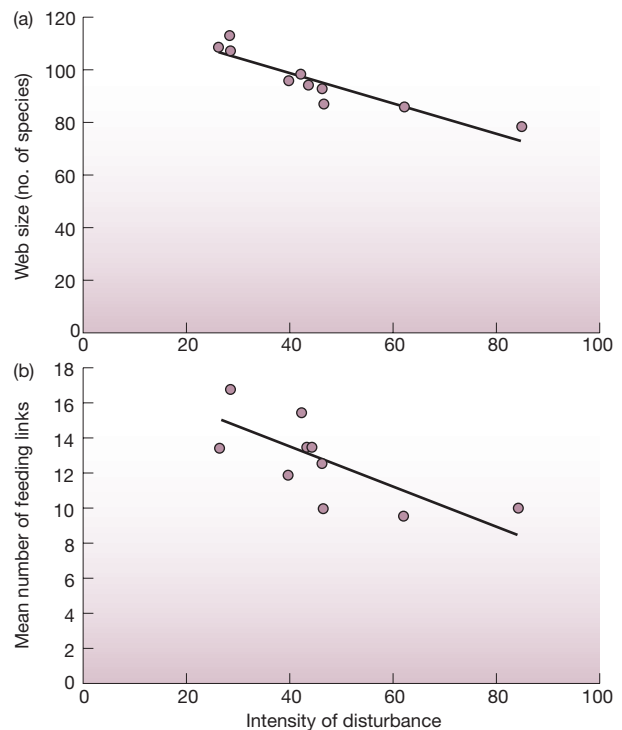
**Figure 9.25**

The results of a simulation study. The effect of sequential species removal on the number of consequential (secondary) species extinctions, as a proportion of the total number of species originally in the web,  $S$ , for each of 16 previously described food webs. The three different rules for species removal are described in the lower panel. Robustness of the webs (the tendency *not* to suffer secondary extinctions) was usually lowest when the most connected species were removed first and highest when the least connected were removed first.

and so forth) in all communities, since this will depend on the inherent stability of the community combined with the variability of the environment. One study tending to support this investigated 10 small streams in New Zealand that differ in the intensity and frequency of flow-related disturbances to their beds (Figure 9.26). Food webs in the more disturbed, ‘unstable’ streams were characterized by less complex communities: fewer species and fewer links between species.

**Figure 9.26**

In New Zealand streams, less disturbed sites support more 'complex' communities, with (a) more species (greater web size) and (b) greater connectance between species. The average number of feeding links per animal species (number of prey species in the diet) increases with the intensity of flow-related disturbances to the streambed.



AFTER TOWNSEND ET AL., 1998

This line of argument, moreover, carries a further, very important implication for the likely effects of unnatural perturbations caused by humans on communities. We might expect these to have their most profound effects on the dynamically fragile, complex communities of stable environments, which are relatively unaccustomed to perturbations, and least effect on the simple, robust communities of variable environments, which have previously been subjected to repeated (albeit natural) perturbations.



## Summary

### Multiple determinants of the dynamics of populations

To understand the factors responsible for the population dynamics of even a single species in a single location, it is necessary to have a knowledge of physicochemical conditions, available resources, the

organism's life cycle, and the influence of competitors, predators and parasites on rates of birth, death, immigration and emigration.

There are contrasting theories to explain the abundance of populations. At one extreme, researchers emphasize the apparent stability of populations and

point to the importance of forces that stabilize (density-dependent factors). At the other extreme, those who place more emphasis on density fluctuations may look at external (often density-independent) factors to explain the changes. Key factor analysis is a technique that can be applied to life table studies to throw light both on determination and on regulation of abundance.

### Dispersal, patches and metapopulation dynamics

Movement can be a vital factor in determining and/or regulating abundance. A radical change in the way ecologists think about populations has involved focusing attention less on processes occurring within populations and more on patchiness, the colonization and extinction of subpopulations within an overall metapopulation, and dispersal between subpopulations.

### Temporal patterns in community composition

Disturbances that open up gaps (patches) are common in all kinds of community. Founder-controlled communities are those in which all species are approximately equivalent in their ability to invade gaps and are equal competitors that can hold the gaps against all comers during their lifetime. Dominance-controlled communities are those in which some species are competitively superior to others so that an initial colonizer of a patch cannot necessarily maintain its presence there.

The phenomenon of dominance control is responsible for many examples of community succession. Primary successions occur in habitats where no seeds or spores remain from previous occupants of the site: all colonization must be from outside the patch. Secondary successions occur when existing communities are disturbed but some at least of their seed, etc. remain. It can be very difficult to identify when a succession reaches a stable climax community, since this may take centuries to achieve and in the meantime further disturbances are likely to occur. The exact nature of the colonization process in an empty patch depends on the size and location of that

patch. Many communities are mosaics of patches at different stages in a succession.

### Food webs

No predator–prey, parasite–host or grazer–plant pair exists in isolation. Each is part of a complex food web involving other predators, parasites, food sources and competitors within the various trophic levels of a community.

The effect of one species on another (its herbivorous prey) may be direct and straightforward. But indirect effects may also be felt by any of the myriad species linked more remotely in the food web. One of the most common is a ‘trophic cascade’, in which, say, a predator reduces the abundance of a herbivore, thus increasing the abundance of plants.

Top-down control of a food web occurs in situations in which the structure (abundance, species number) of lower trophic levels depends on the effects of consumers from higher trophic levels. Bottom-up control, on the other hand, occurs in a community structure dependent on factors, such as nutrient concentration and prey availability, that influence a trophic level from below. The relative importance of these forces varies according to the trophic level under investigation and the number of trophic levels present.

Some species are more tightly woven into the food web than others. A species whose removal would produce a significant effect (extinction or a large change in density) in at least one other species may be thought of as a strong interactor. Removal of some strong interactors leads to significant changes that spread throughout the food web; we refer to these as keystone species.

The relationship between food web complexity and stability is uncertain (and care is needed in deciding what is meant by stability). Mathematical and empirical studies agree in suggesting that, if anything, population stability decreases with complexity, whereas the stability of aggregate properties of whole communities increases with complexity, especially species richness.

## Review questions

### REVIEW QUESTIONS

Asterisks indicate challenge questions

- 1\* Construct a flow diagram (boxes and arrows) with a named population at its center to illustrate the wide range of abiotic and biotic factors that influence its pattern of abundance.
- 2 Population census data can be used to establish correlations between abundance and external factors such as weather. Why can such correlations not be used to prove a causal relationship that explains the dynamics of the population?
- 3 Distinguish between the determination and regulation of population abundance.
- 4\* Imagine a number of species with patchy distributions: a plant, an insect and a mammal – or consider examples of such species with which you are familiar. How would you identify ‘habitable patches’ of these species that are not currently occupied by them?
- 5 What is meant by a ‘metapopulation’ and how does it differ from a simple ‘population’?
- 6 Define founder control and dominance control as they apply to community organization. In a mosaic of habitat patches, how would you expect communities to differ if they were dominated by founder or dominance control?
- 7 What factors are responsible for changes in species composition during an old-field succession?
- 8\* Draw up a food web of, say, six or seven species with which you are familiar and which spans at least three trophic levels. Take each species in turn and suggest the kind of community organization that would be necessary for this to be a keystone species.
- 9 What are meant by bottom-up and top-down control? How is the importance of each likely to vary with the number of trophic levels in a community?
- 10 Discuss what is understood about the relationship between the complexity and stability of food webs.

# Chapter 10



## Patterns in species richness

### *Chapter contents*

#### CHAPTER CONTENTS

- 10.1 Introduction
- 10.2 A simple model of species richness
- 10.3 Spatially varying factors that influence species richness
- 10.4 Temporally varying factors that influence species richness
- 10.5 Gradients of species richness
- 10.6 Patterns in taxon richness in the fossil record
- 10.7 Appraisal of patterns in species richness

### *Key concepts*

#### KEY CONCEPTS

In this chapter you will:

- understand the meanings of species richness, diversity indices and rank–abundance diagrams
- appreciate that species richness is limited by available resources, the average portion of the resources used by each species (niche breadth) and the degree of overlap in resource use
- recognize that species richness may be highest at intermediate levels of productivity, predation intensity or disturbance but tends to increase with spatial heterogeneity
- appreciate the importance of habitat area and remoteness in determining richness, especially with reference to the equilibrium theory of island biogeography
- understand richness gradients with latitude, altitude and depth, and during community succession, and the difficulties of explaining them
- appreciate how theories of species richness can also be applied to the fossil record

*An accurate appreciation of the world's biological diversity is becoming increasingly important. For our conservation efforts to be effective we must understand why species richness varies widely across the face of the Earth. Why do some communities contain more species than others? Are there patterns or gradients in this biodiversity? If so, what are the reasons for these patterns?*

## 10.1 Introduction

Why the number of species varies from place to place, and from time to time, are questions that present themselves not only to ecologists but to anybody who observes and ponders the natural world. They are interesting questions in their own right – but they are also questions of practical importance. It is clear that if we wish to conserve or restore the planet's biological diversity, then we must understand how species numbers are determined and how it comes about that they vary. We will see that there are plausible answers to the questions we ask, but these answers are not always clearcut. Yet this is not so much a disappointment as a challenge to ecologists of the future. Much of the fascination of ecology lies in the fact that many of the problems are blatant, whereas the solutions can be difficult to find. We will see that a full understanding of patterns in species richness must draw on our knowledge of all the areas of ecology discussed so far in this book.

determining species richness

The number of species in a community is referred to as its *species richness*. Counting or listing the species present in a community may sound a straightforward procedure, but in practice it is often surprisingly difficult, partly because of taxonomic inadequacies, but also because only a proportion of the organisms in an area can usually be counted. The number of species recorded then depends on the number of samples that have been taken, or on the volume of the habitat that has been explored. The most common species are likely to be represented in the first few samples, and as more samples are taken, rarer species will be added to the list. At what point does one cease to take further samples? Ideally, the investigator should continue to sample until the number of species reaches a plateau. At the very least, the species richness of different communities should be compared only if they are based on the same sample sizes (in terms of area of habitat explored, time devoted to sampling or, best of all, number of individuals included in the samples).

diversity indices and  
rank–abundance diagrams

An important aspect of the structure of a community is completely ignored, though, when its composition is described simply in terms of the number of species present – namely, that some species are rare and others common. Intuitively, a community of 10 species with equal numbers in each seems more diverse than another, again consisting of 10 species, with 91% of the individuals belonging to the most common species and just 1% in each of the other nine species. Yet, each community has the same species richness. *Diversity indices* are designed to combine both species richness and the evenness or equitability of the distribution

of individuals among those species (Box 10.1). Moreover, attempts to describe a complex community structure by one single attribute, such as richness, or even diversity, can still be criticized because so much valuable information is lost. A more complete picture of the distribution of species abundance in a community is therefore sometimes provided in a *rank–abundance diagram* (Box 10.1).



## 10.1 QUANTITATIVE ASPECTS

### 10.1 Quantitative aspects

#### Diversity indices and rank–abundance diagrams

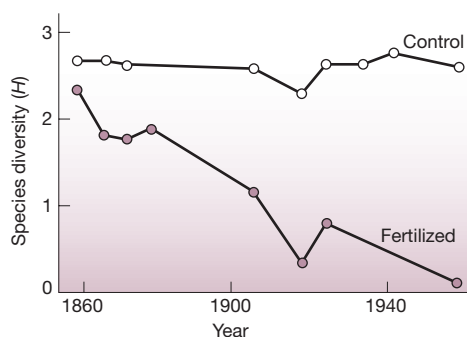
The measure of the character of a community that is most commonly used to take into account both species richness and the relative abundances of those species is known as the *Shannon* or the *Shannon–Weaver diversity index* (denoted by  $H$ ). This is calculated by determining, for each species, the proportion of individuals or biomass ( $P_i$  for the  $i$ th species) that that species contributes to the total in the sample. Then, if  $S$  is the total number of species in the community (i.e. the richness), diversity ( $H$ ) is:

$$H = -\sum P_i \ln P_i$$

where the summation sign  $\sum$  indicates that the product ( $P_i \ln P_i$ ) is calculated for each of the  $S$  species in turn and these products are then summed. As required, the value of the index depends on both the species richness and the evenness (equitability) with which individuals are distributed among the species. Thus, for a given richness,  $H$  increases with equitability, and for a given equitability,  $H$  increases with richness.

An example of an analysis using diversity indices is provided by the unusually long-term study that commenced in 1856 in an area of pasture at Rothamsted in England. Experimental plots received a fertilizer treatment once every year, and control plots did not. Figure 10.1 shows how species diversity ( $H$ ) of grass species changed between 1856 and 1949. While the unfertilized area remained essentially unchanged, the fertilized area showed a progressive decline in diversity. This ‘paradox of enrichment’ is discussed in Section 10.3.1.

Rank–abundance diagrams, on the other hand, make use of the full array of  $P_i$  values by plotting  $P_i$



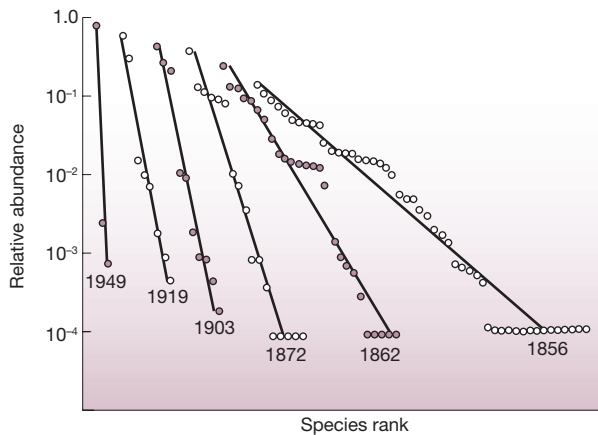
**Figure 10.1**

Species diversity ( $H$ ) declined progressively in a plot of pasture that regularly received fertilizer in an experiment commencing in 1856 at Rothamsted in England. In contrast, species diversity remained constant in a control plot that received no fertilizer.

AFTER TILMAN, 1982

against ‘rank’; i.e. the most abundant species takes rank 1, the second most abundant rank 2, and so on, until the array is completed by the rarest species of all. The steeper the slope of a rank–abundance diagram, the greater the dominance of common species over rare species in the community (a steep slope means a sharp drop in relative abundance,  $P_i$ , for a given drop in rank). Thus, in the case of the Rothamsted experiment, Figure 10.2 shows how the dominance of commoner species steadily increased (steeper slope) while species richness decreased over time.





**Figure 10.2**

Change in the rank–abundance pattern of plant species in the Rothamsted fertilized plot from 1856 to 1949. Note how the slope of the regression line becomes progressively steeper with time since commencement of fertilizer addition. A steeper plot indicates that the commoner species comprise a greater proportion of the total community – in other words, this pasture community gradually became dominated by just a few species.

AFTER TOKESHI, 1993

Nonetheless, for many purposes, the simplest measure, species richness, suffices. In the following sections, therefore, we examine the relationships between species richness and a variety of factors that may, in theory, influence richness in ecological communities. It will become clear that it is not always easy to come up with unambiguous predictions and clean tests of hypotheses when dealing with something as complex as a community.

## 10.2 A simple model of species richness

To try to understand the determinants of species richness, it will be useful to begin with a simple model (Figure 10.3). Assume, for simplicity, that the resources available to a community can be depicted as a one-dimensional continuum,  $R$  units long. Each species uses only a portion of this resource continuum, and these portions define the *niche breadths* ( $n$ ) of the various species: the average niche breadth within the community is  $\bar{n}$ . Some of these niches overlap, and the overlap between adjacent species can be measured by value  $o$ . The average niche overlap within the community is then  $\bar{o}$ . With this simple background, it is possible to consider why some communities should contain more species than others.

First, for given values of  $\bar{n}$  and  $\bar{o}$ , a community will contain more species the larger the value of  $R$ , i.e. the greater the range of resources (Figure 10.3a). Second, for a given range of resources, more species will be accommodated if  $\bar{n}$  is smaller, i.e. if the species are more specialized in their use of resources (Figure 10.3b). Alternatively, if species overlap to a greater extent in their use of resources (greater  $\bar{o}$ ), then more may coexist along the same resource continuum (Figure 10.3c). Finally, a community will contain more species the more fully saturated it is; conversely, it will contain fewer species when more of the resource continuum is unexploited (Figure 10.3d).

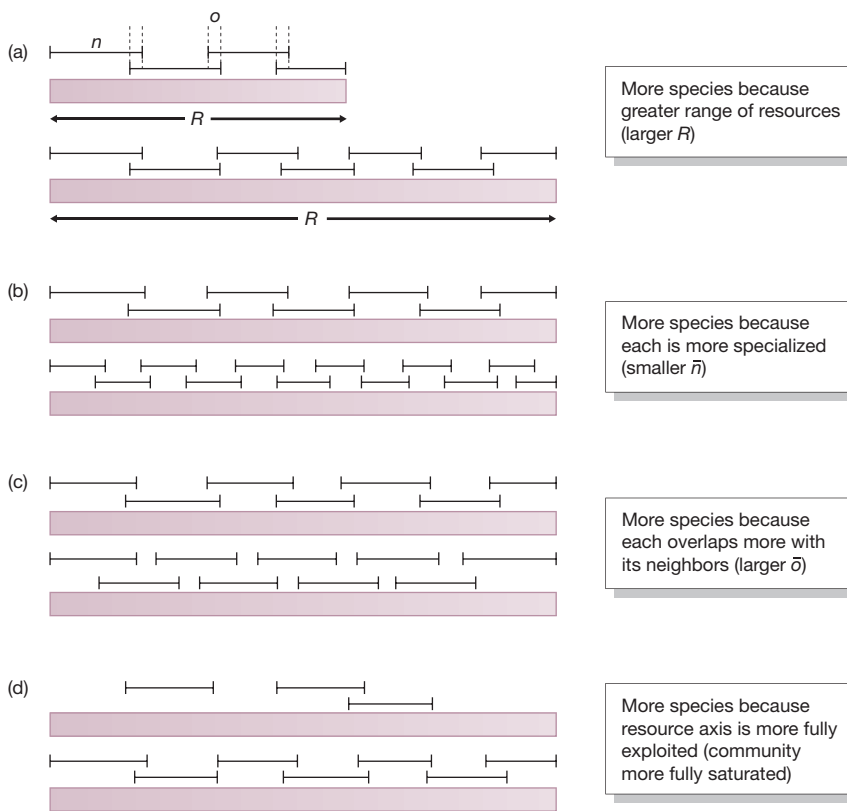


Figure 10.3

A simple model of species richness. Each species utilizes a portion  $n$  of the available resources ( $R$ ), overlapping with adjacent species by an amount  $o$ . More species may occur in one community than in another because: (a) a greater range of resources is present (larger  $R$ ), (b) each species is more specialized (smaller average  $n$ ), (c) each species overlaps more with its neighbors (larger average  $o$ ), or (d) the resource dimension is more fully exploited.

AFTER MACARTHUR, 1972

We can now consider the relationship between this model and two important kinds of species interactions described in previous chapters: interspecific competition and predation. If a community is dominated by interspecific competition (see Chapter 6), the resources are likely to be fully exploited. Species richness will then depend on the range of available resources, the extent to which species are specialists and the permitted extent of niche overlap (Figure 10.3a–c). We will examine a range of influences on each of these three.

Predation, on the other hand, is capable of exerting contrasting effects (see Chapter 7). First, we know that predators can exclude certain prey species; in the absence of these species the community may then be less than fully saturated, in the sense that some available resources may be unexploited (Figure 10.3d). In this way, predation may reduce species richness. Second though, predation may tend to keep species below their carrying capacities for much of the time, reducing the intensity and importance of direct interspecific competition for resources. This may then permit much more niche overlap and a *greater* richness of species than in a community dominated by competition (Figure 10.3c).

The next two sections examine a variety of factors that influence species richness. To organize these, Section 10.3 focuses on factors that often vary spatially (from place to place): productivity, predation intensity, spatial heterogeneity and environmental ‘harshness’. Section 10.4 then focuses on factors reflecting temporal variation: climatic variation, disturbance and evolutionary age.

competition and predation may influence species richness

## 10.3 Spatially varying factors that influence species richness

### 10.3.1 Productivity and resource richness

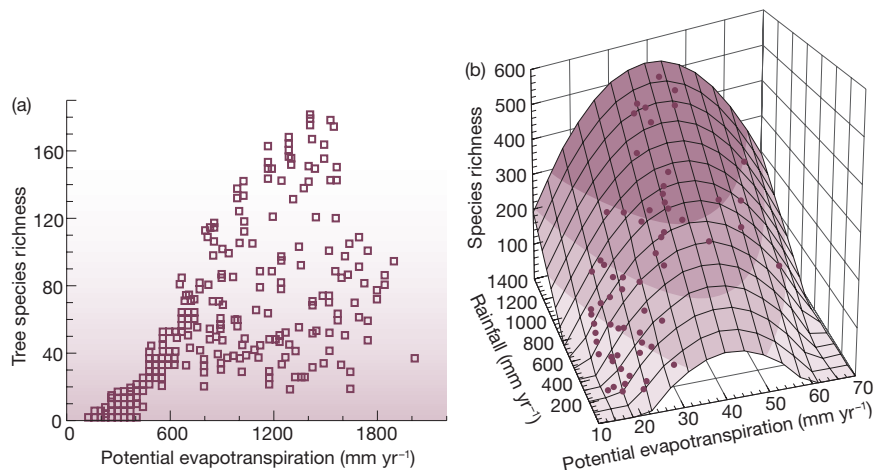
For plants, the productivity of the environment can depend on whichever nutrient or condition is most limiting to growth (dealt with in detail in Chapter 11). Broadly speaking, the productivity of the environment for animals follows the same trends as for plants, mainly as a result of the changes in resource levels at the base of the food chain.

If higher productivity is correlated with a wider *range* of available resources, then this is likely to lead to an increase in species richness (Figure 10.3a). However, a more productive environment may have a higher rate of supply of resources but not a greater variety of resources. This might lead to more individuals per species rather than more species. Alternatively again, it is possible, even if the overall variety of resources is unaffected, that rare resources in an unproductive environment may become abundant enough in a productive environment for extra species to be added, because more specialized species can be accommodated (Figure 10.3b).

In general, though, we might expect species richness to increase with productivity – a contention that is supported by an analysis of the species richness of trees in North America in relation to a crude measure of available environmental energy, *potential evapotranspiration* (PET). This is the amount of water that under prevailing conditions would evaporate or be transpired from a saturated surface (Figure 10.4a). However, while energy (heat and light) is

increased productivity might be expected to lead to increased richness . . .

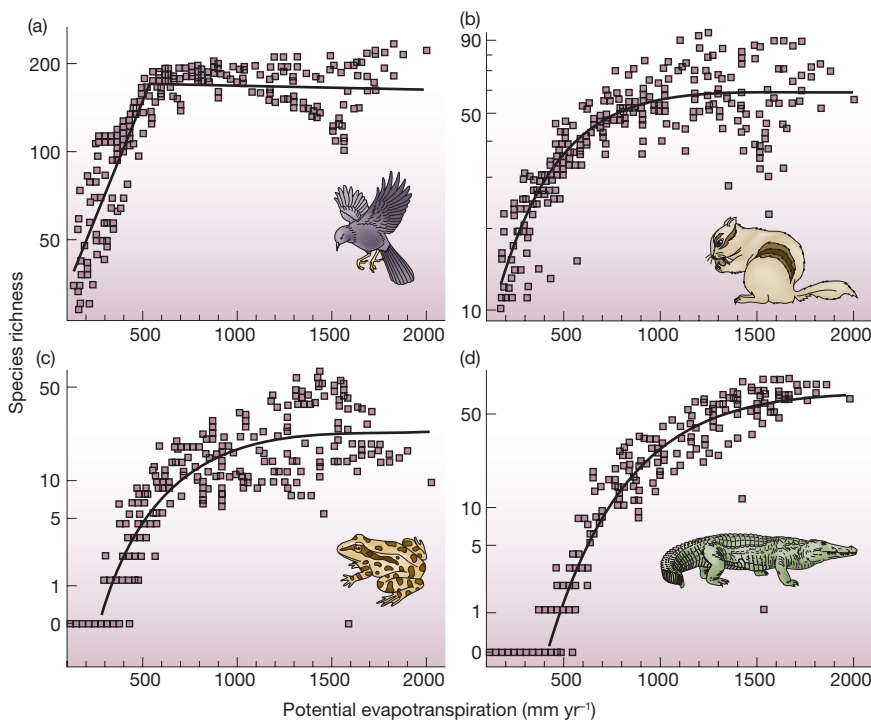
. . . and often does



**Figure 10.4**

(a) Species richness of trees in North America (north of the Mexican border) in relation to potential evapotranspiration. For this analysis the continent was divided into 336 quadrats following lines of latitude and longitude. (b) Species richness of southern African trees (each dot represents a 25,000 km<sup>2</sup> map quadrat) in relation to both rainfall and potential evapotranspiration. The three-dimensional surface describes the regression relationship of species richness with rainfall and potential evapotranspiration. The surface is divided into zones of increasing depth of color representing increasing species richness.

(a) AFTER CURRIE & PAQUIN, 1987; CURRIE, 1991; (b) DATA FROM O'BRIEN, 1993; AFTER WHITTAKER ET AL., 2003

**Figure 10.5**

Species richness of: (a) birds, (b) mammals, (c) amphibians and (d) reptiles in North America in relation to potential evapotranspiration.

AFTER CURRIE, 1991

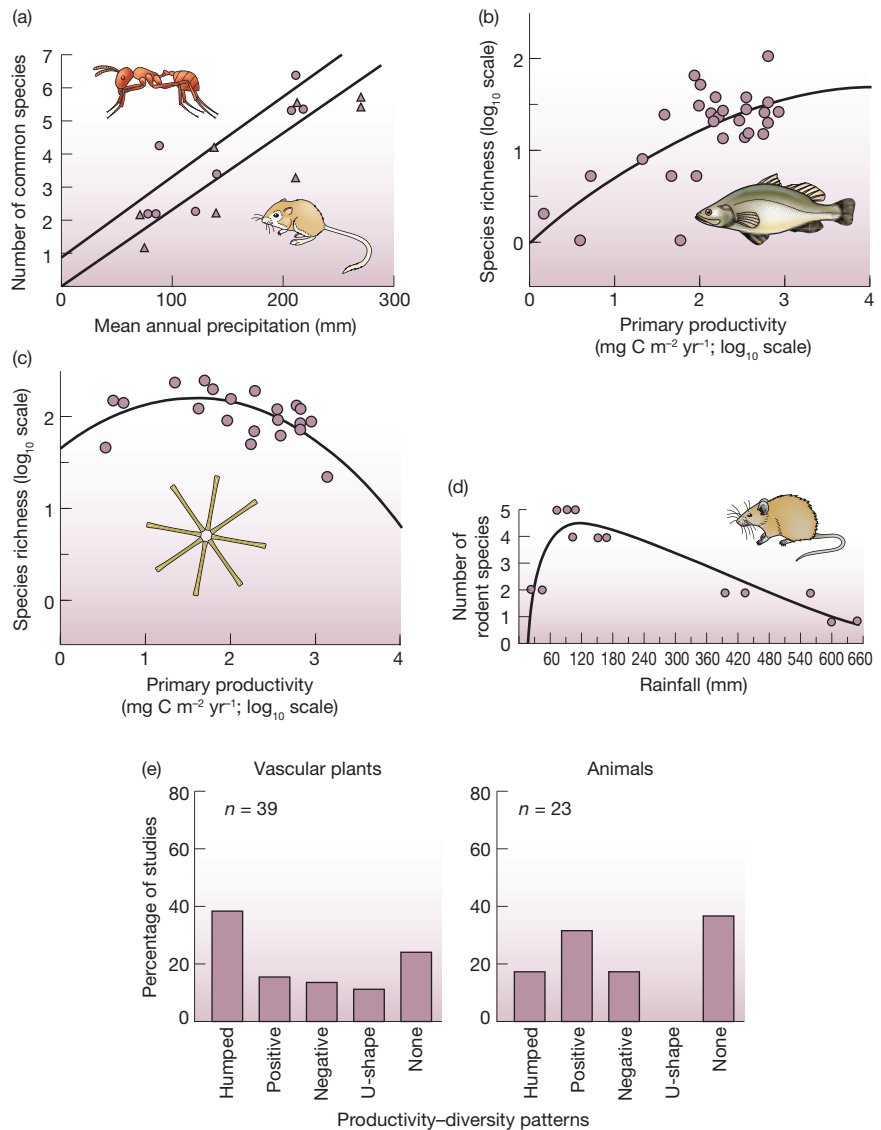
necessary for tree functioning, plants also depend critically on actual water availability. Indeed, energy and water availability inevitably interact, since higher energy inputs lead to more evapotranspiration and a greater requirement for water (Whittaker et al., 2003). Thus, in a study of southern African trees, species richness increased with water availability (annual rainfall), but first increased and then decreased with available energy (PET; Figure 10.4b). Such hump-shaped richness patterns will be a recurring feature in this chapter.

When the North American work (Figure 10.4a) was extended to four vertebrate groups, species richness correlated to some extent with tree species richness itself. However, the best correlations were consistently with PET (Figure 10.5). Why should animal species richness be positively correlated with crude atmospheric energy? The answer is not known with any certainty, but it may be because for an ectotherm, such as a reptile, extra atmospheric warmth would enhance the intake and utilization of food resources; while for an endotherm, such as a bird, the extra warmth would mean less expenditure of resources in maintaining body temperature and more available for growth and reproduction. In both cases, then, this could lead to faster individual and population growth and thus to larger populations. Warmer environments might therefore allow species with narrower niches to persist and such environments may therefore support more species in total (Turner et al., 1996) (see Figure 10.3b).

Sometimes there seems to be a direct relationship between animal species richness and plant productivity. Thus, there are strong positive correlations between species richness and precipitation for both seed-eating ants and seed-eating rodents in the southwestern deserts of the United States (Figure 10.6a). In such arid regions, it is well established that mean annual precipitation is closely related

**Figure 10.6**

Relationships between species richness and productivity. Where best-fit lines are shown (see Box 1.2), each is statistically significant. (a) The species richness of seed-eating rodents (triangles) and ants (circles) inhabiting sandy soils increased along a geographic gradient of increasing precipitation and, therefore, of increasing productivity. (b) Species richness of fish increased with primary productivity of phytoplankton in a series of North American lakes, while (c) species richness of the phytoplankton themselves showed a hump-shaped relationship, increasing with productivity when productivity was low, but declining at higher levels. (d) Species richness of desert rodents also showed a hump-shaped relationship when plotted against annual rainfall. (e) Percentage of published studies on plants and animals showing various patterns between species richness and productivity. All conceivable patterns have been detected, but hump-shaped and positive patterns, such as those shown in (a) to (d), are well represented. However, it is not uncommon for no pattern to be documented.



to plant productivity and thus to the amount of seed resource available. It is particularly noteworthy that in species-rich sites, the communities contain more species of very large ants (which consume large seeds) and more species of very small ants (which take small seeds) (Davidson, 1977). It seems that either the range of seed sizes is greater in the more productive environments (Figure 10.3a) or the abundance of seeds becomes sufficient to support extra consumer species with narrower niches (Figure 10.3b). The species richness of fish in North American lakes also increases with an increase in productivity of the lake's phytoplankton (Figure 10.6b).

On the other hand, an increase in diversity with productivity is by no means universal, as shown for example, by the unique experiment that started in 1856 at Rothamsted in England (see Box 10.1). An 8 acre pasture was divided into

other evidence shows richness declining with productivity . . .

20 plots, two serving as controls and the others receiving a fertilizer treatment once a year. While the unfertilized areas remained essentially unchanged, the fertilized areas showed a progressive decline in species richness (and diversity).

Such declines have long been recognized. Rosenzweig (1971) referred to them as illustrating “the paradox of enrichment”. One possible resolution of the paradox is that high productivity leads to high rates of population growth, bringing about the extinction of some of the species present because of a speedy conclusion to any potential competitive exclusion (see Section 6.2.7). At lower productivity, the environment is more likely to have changed before competitive exclusion is achieved. An association between high productivity and low species richness has been found in several other studies of plant communities (reviewed by Tilman, 1986). It can be seen, for example, where human activities lead to an increased input of plant resources like nitrates and phosphates into lakes, rivers, estuaries and coastal marine regions; when such ‘cultural eutrophication’ is severe, we consistently see a decrease in species richness of phytoplankton (despite an increase in their productivity).

It is perhaps not surprising, then, that several studies have demonstrated both an increase and a decrease in richness with increasing productivity – that is, that species richness may be highest at intermediate levels of productivity. Species richness declines at the lowest productivities because of a shortage of resources, but also declines at the highest productivities where competitive exclusions speed rapidly to their conclusion. For instance, there are humped curves when the number of lake phytoplankton species is plotted against overall phytoplankton productivity (Figure 10.6c; the decline at higher productivity is analogous to the cultural eutrophication mentioned above) and when the species richness of desert rodents is plotted against precipitation (and thus productivity) along a geographic gradient in Israel (Figure 10.6d). Indeed, an analysis of a wide range of such studies found that when communities differing in productivity but of the same general type (e.g. tallgrass prairie) were compared (Figure 10.6e), a positive relationship was the most common finding in animal studies (with fair numbers of humped and negative relationships), whereas with plants, humped relationships were most common, with smaller numbers of positives and negatives (and even some U-shaped curves – cause unknown!). Clearly, increased productivity can and does lead to increased or decreased species richness – or both.

... and further evidence suggests a ‘humped’ relationship

### 10.3.2 Predation intensity

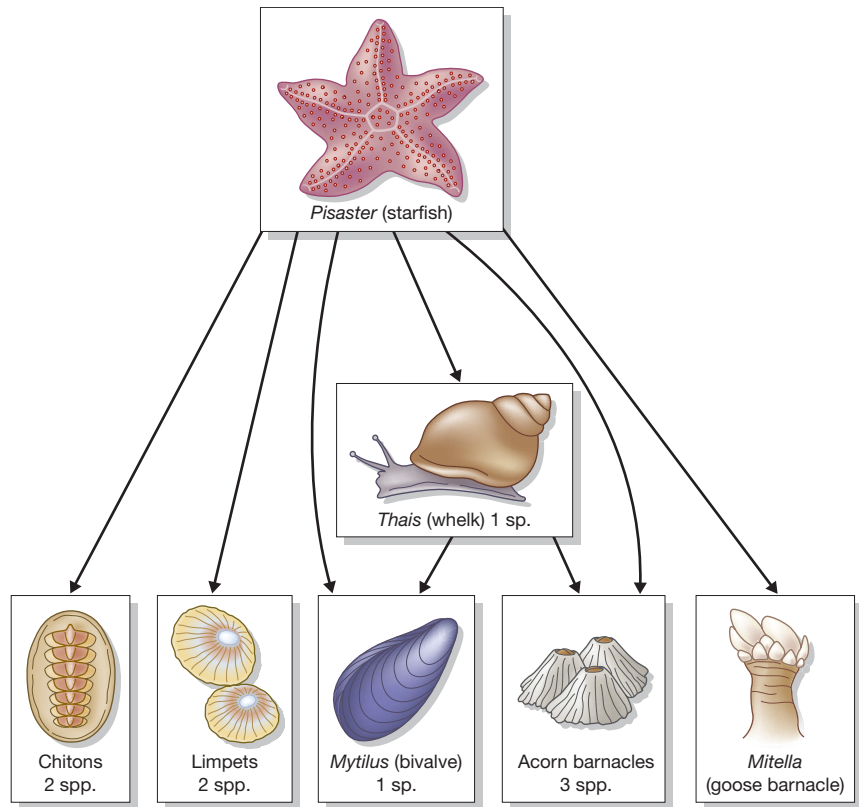
The possible effects of predation on the species richness of a community were examined in Chapter 7: predation may increase richness by allowing otherwise competitively inferior species to coexist with their superiors (*predator-mediated coexistence*); but intense predation may reduce richness by driving prey species (whether or not they are strong competitors) to extinction. Overall, therefore, there may also be a humped relationship between predation intensity and species richness in a community, with greatest richness at intermediate intensities, such as that shown by the effects of cattle grazing (illustrated in Figure 7.24).

A classic example of predator-mediated coexistence is provided by a study that established the concept in the first place: the work of Paine (1966) on the influence of a top carnivore on community structure on a rocky shore (Figure 10.7).

predator-mediated coexistence by starfish on a rocky shore

**Figure 10.7**

Paine's rocky shore community. The profound influence of the predatory starfish could only be detected by removing them. In the absence of *Pisaster*, other species became dominant (first barnacles and then mussels) leading to an overall reduction in species richness. This is a classic case of predator-mediated coexistence.



AFTER PAINE, 1966

The starfish *Pisaster ochraceus* preys on sessile filter-feeding barnacles and mussels, and also on browsing limpets and chitons and a small carnivorous whelk. These species, together with a sponge and four macroscopic algae (seaweeds), form a typical community on rocky shores of the Pacific coast of North America. Paine removed all starfish from a stretch of shoreline about 8 m long and 2 m deep and continued to exclude them for several years. The structure of the community in nearby control areas remained unchanged during the study, but the removal of *Pisaster* had dramatic consequences. Within a few months, the barnacle *Balanus glandula* settled successfully. Later mussels (*Mytilus californicus*) crowded it out, and eventually the site became dominated by these. All but one of the species of alga disappeared, apparently through lack of space, and the browsers tended to move away, partly because space was limited and partly because there was a lack of suitable food. The main influence of the starfish *Pisaster* appears to be to make space available for competitively subordinate species. It cuts a swathe free of barnacles and, most importantly, free of the dominant mussels that would otherwise outcompete other invertebrates and algae for space. Overall, there is usually predator (starfish)-mediated coexistence, but the removal of starfish led to a reduction in number of species from 15 to eight. The concept of predator-mediated coexistence is not only intrinsically interesting; it also finds a surprising application in the field of restoration ecology (Box 10.2).





## 10.2 TOPICAL ECONCERNS

### 10.2 Topical ECONcerns

#### Using exploiter-mediated coexistence to assist grassland restoration

Species-rich meadows are now uncommon in agricultural landscapes in Europe because decades of intensive fertilizer application have allowed a few species to competitively exclude others, a pattern that echoes the results of the remarkable century-long Rothamsted experiment (see Figure 10.1). It is not uncommon nowadays for attempts to be made to restore the lost species richness of these pasture settings. One approach is to use what we know about predator-mediated coexistence or, more generally, exploiter-mediated coexistence. This occurs when one species ‘exploits’ as food a number of species in the community, reducing the dominance of the most competitively superior species and allowing less competitive species to maintain a foothold.

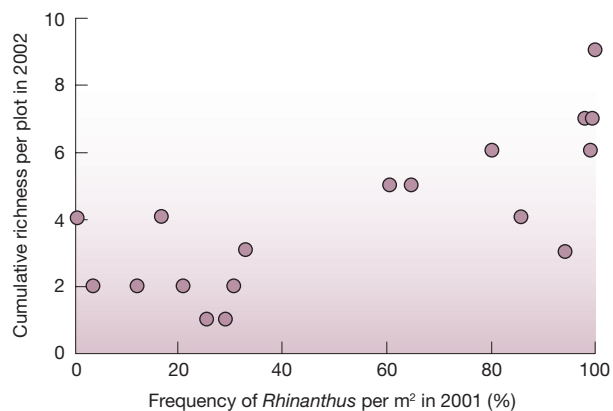
One example of exploiter-mediated coexistence occurs when parasites exert a leveling effect. *Rhinanthus minor*, an annual plant, is capable of its own limited

photosynthesis but is known as a ‘hemiparasite’ because it typically taps into the photosynthetic products of other plants by building connections with their roots. Researchers reasoned that the presence of the hemiparasite might facilitate recovery to species-rich grassland via exploiter-mediated coexistence (Pywell et al., 2004). To test this hypothesis in an agriculturally impoverished grassland, they established experimental plots with various densities of *Rhinanthus minor*. After the hemiparasite populations had become established, the researchers sowed a mixture of seeds of 10 native wildflower species that had been lost from the grassland as a result of intensive agriculture. After 2 years the hemiparasite was found to have suppressed the growth of the parasitized plants and this led, the following year, to the desired increase in grassland species richness because competitive exclusion had been circumvented (Figure 10.8).



A species-rich flower meadow

© ALAMY IMAGES A4T6HC



**Figure 10.8**

Relationship between frequency of occurrence of the hemiparasite *Rhinanthus minor* and species richness of plants per experimental plot of grassland. The presence of the hemiparasite leads to lower plant height, because of reduced success of the parasitized plants, and the following year to increased species richness because of suppression of competitive exclusion by the dominant species.

(LEFT) © ALAMY IMAGES A02Y49; (RIGHT) AFTER PYWELL ET AL., 2004

*An understanding of exploiter-mediated coexistence holds promise for future meadow restoration efforts. Can you think of any other aspects of the theory of species richness that could be applied to the benefit of impoverished grasslands? (Clue – check out the ‘intermediate disturbance hypothesis’, described in*

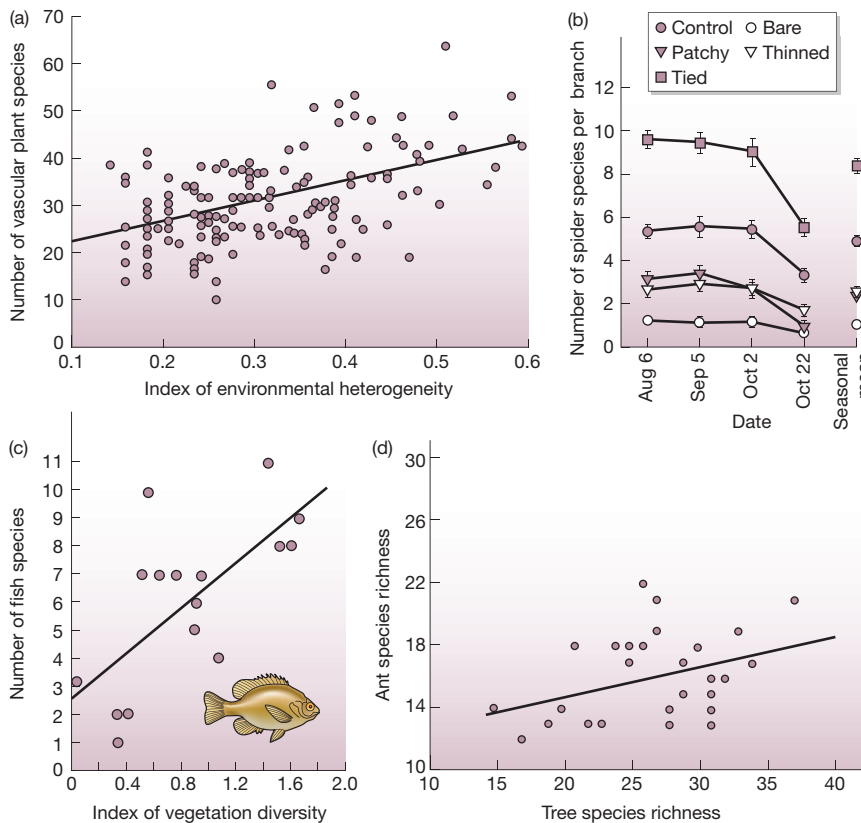
*Section 10.4.2. These intensively farmed landscapes have also been subject to regular and intensive disturbances caused by heavy mowing or grazing. What might the intermediate disturbance hypothesis have to offer in restoring grassland species richness?)*

### 10.3.3 Spatial heterogeneity

Environments that are more spatially heterogeneous can be expected to accommodate extra species because they provide a greater variety of microhabitats, a greater range of microclimates, more types of places to hide from predators, and so on. In effect, the extent of the resource spectrum is increased (see Figure 10.3a).

In some cases, it has been possible to relate species richness to the spatial heterogeneity of the abiotic environment. For instance, a study of plant species growing in 51 plots alongside the Hood River, Canada, revealed a positive relationship

richness and the heterogeneity  
of the abiotic environment

**Figure 10.9**

(a) Relationship between the number of plants per 300 m<sup>2</sup> plot beside the Hood River, Northwest Territories, Canada, and an index (ranging from 0 to 1) of spatial heterogeneity in abiotic factors associated with topography and soil. (b) In an experimental study, the number of spider species living on Douglas fir branches increased with their structural diversity. Those 'bare', 'patchy' or 'thinned' were less diverse than normal ('control') by virtue of having needles removed; those 'tied' were more diverse because their twigs were entwined together. (c) Relationship between animal species richness and an index of structural diversity of vegetation for freshwater fish in 18 Wisconsin lakes. (d) Relationship between arboreal ant species richness in Brazilian savanna and the species richness of trees (a surrogate for spatial heterogeneity).

between species richness and an index of spatial heterogeneity (based, among other things, on the number of categories of substrate, slope, drainage regimes and soil pH present) (Figure 10.9a).

Most studies of spatial heterogeneity, though, have related the species richness of animals to the structural diversity of the plants in their environment, either as a result of experimental manipulation of the plants, as with the spiders in Figure 10.9b, but more commonly through comparisons of natural communities that differ in plant structural diversity (Figure 10.9c) or plant species richness (where higher species richness equates to greater spatial heterogeneity; Figure 10.9d).

Whether spatial heterogeneity arises from the abiotic environment or is provided by biological components of the community, it is capable of promoting an increase in species richness.

### 10.3.4 Environmental harshness

Environments dominated by an extreme abiotic factor – often called *harsh* environments – are more difficult to recognize than might be immediately apparent. An anthropocentric view might describe as extreme both very cold and very hot habitats, unusually alkaline lakes and grossly polluted rivers. However, species have evolved and live in all such environments, and what is very cold and extreme for us must seem benign and unremarkable to a penguin.

animal richness and plant spatial heterogeneity

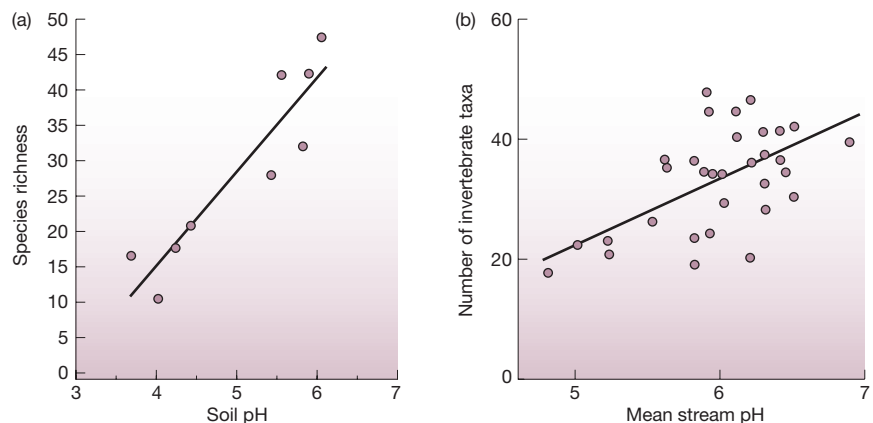
We might try to get around the problem of defining environmental harshness by ‘letting the organisms decide’. An environment may be classified as *extreme* if organisms, by their failure to live there, show it to be so. But if the claim is to be made – as it often is – that species richness is lower in extreme environments, then this definition is circular, and it is designed to prove the very claim we wish to test.

Perhaps the most reasonable definition of an extreme condition is one that requires, of any organism tolerating it, a morphological structure or biochemical mechanism that is not found in most related species and is costly, either in energetic terms or in terms of the compensatory changes in the biological processes of the organism that are needed to accommodate it. For example, plants living in highly acidic soils (low pH) may be affected directly through injury by hydrogen ions or indirectly via deficiencies in the availability and uptake of important resources such as phosphorus, magnesium and calcium. In addition, aluminum, manganese and heavy metals may have their solubility increased to toxic levels. Moreover, the activity of symbiotic fungi (mycorrhizas enhancing uptake of dissolved nutrients – see Section 8.4.5) or bacteria (fixation of atmospheric nitrogen – see Section 8.4.6) may be impaired. Plants can only tolerate low pH if they have specific structures or mechanisms allowing them to avoid or counteract these effects.

Environments that experience low pHs can thus be considered harsh, and the mean number of plant species recorded per sampling unit in a study in the Alaskan Arctic tundra was indeed lowest in soils of low pH (Figure 10.10a). Similarly, the species richness of benthic (bottom-dwelling) invertebrates in streams in southern England was markedly lower in the more acidic streams (Figure 10.10b). Further examples of extreme environments that are associated with low species richness include hot springs, caves and highly saline water bodies such as the Dead Sea. The problem with these examples, however, is that each is also characterized by other features associated with low species richness, such as low productivity and low spatial heterogeneity. In addition, many occupy small areas (caves, hot springs) or areas that are rare compared to other types of habitat (only a small proportion of the streams in southern England are acidic). Hence extreme environments can often be seen as small and isolated islands.

**Figure 10.10**

(a) The number of plant species in the Alaskan Arctic tundra increases with soil pH. (b) The number of taxa of invertebrates in streams in southern England increases with the pH of stream water.



We will see in Section 10.5.1 that these features, too, are usually associated with low species richness. Although it appears reasonable that intrinsically extreme environments should as a consequence support few species, this has proved an extremely difficult proposition to establish.

## 10.4 Temporally varying factors that influence species richness

Temporal variation in conditions and resources may be predictable or unpredictable and operate on time scales from minutes through to centuries and millennia. All may influence species richness in profound ways.

### 10.4.1 Climatic variation

The effects of climatic variation on species richness depend on whether the variation is predictable or unpredictable (measured on time scales that matter to the organisms involved). In a predictable, seasonally changing environment, different species may be suited to conditions at different times of the year. More species might therefore be expected to coexist in a seasonal environment than in a completely constant one (see Figure 10.3a). Different annual plants in temperate regions, for instance, germinate, grow, flower and produce seeds at different times during a seasonal cycle; while phytoplankton and zooplankton pass through a seasonal succession in large, temperate lakes with a variety of species dominating in turn as changing conditions and resources become suitable for each.

temporal niche differentiation in seasonal environments

On the other hand, there are opportunities for specialization in a non-seasonal environment that do not exist in a seasonal environment. For example, it would be difficult for a specialist fruit-eater to persist in a seasonal environment when fruit is available for only a very limited portion of the year. But such specialization is found repeatedly in non-seasonal, tropical environments where fruit of one type or another is available continuously.

specialization in non-seasonal environments

Unpredictable climatic variation (climatic instability) could have a number of effects on species richness. On the one hand: (i) stable environments may be able to support specialized species that would be unlikely to persist where conditions or resources fluctuated dramatically (Figure 10.3b); (ii) stable environments are more likely to be saturated with species (Figure 10.3d); and (iii) theory suggests that a higher degree of niche overlap will be found in more stable environments (Figure 10.3c). All these processes could increase species richness. On the other hand, populations in a stable environment are more likely to reach their carrying capacities, the community is more likely to be dominated by competition, and species are therefore more likely to be excluded by competition ( $\bar{o}$  is smaller, see Figure 10.3c).

Some studies seem to support the notion that species richness increases as climatic variation decreases. For example, there is a significant negative relationship between species richness and the range of monthly mean temperatures for birds, mammals and gastropods that inhabit the West coast of North America (from Panama in the south to Alaska in the north) (MacArthur, 1975). However,

this correlation does not prove causation, since there are many other things that change between Panama and Alaska. There is no established relationship between climatic instability and species richness.

### 10.4.2 Disturbance

Previously, in Section 9.4, the influence of disturbance on community structure was examined, and it was demonstrated that when a disturbance opens up a gap, and the community is *dominance controlled* (strong competitors can replace residents), there tends in a community succession to be an initial increase in richness as a result of colonization, but a subsequent decline in richness as a result of competitive exclusion.

the intermediate disturbance hypothesis . . .

If the frequency of disturbance is now superimposed on this picture, it seems likely that very frequent disturbances will keep most patches in the early stages of succession (where there are few species) but also that very rare disturbances will allow most patches to become dominated by the best competitors (where there are also few species). This suggests an *intermediate disturbance hypothesis*, in which communities are expected to contain most species when the frequency of disturbance is neither too high nor too low (Connell, 1978). The intermediate disturbance hypothesis was originally proposed to account for patterns of richness in tropical rain forests and coral reefs. It has occupied a central place in the development of ecological theory because all communities are subject to disturbances that exhibit different frequencies and intensities.

. . . supported by studies of algae on boulders on a rocky shore . . .

Among a number of studies that have provided support for this hypothesis, we turn first to a study of green and red algae on different-sized boulders on the rocky shores of southern California (Sousa, 1979a, 1979b). Wave action disturbs small boulders more frequently than larger ones; thus, small boulders had a monthly probability of movement of 42%, intermediate-sized boulders a probability of 9%, and large boulders a probability of only 0.1%. After a disturbance clears space on a boulder, ephemeral green algae (*Ulva* spp.) are quick to colonize, but later in the year several species of perennial red alga feature in the succession, including *Gelidium coulteri*, *Gigartina leptorhynchus*, *Rhodoglossum affine* and *Gigartina canaliculata*. The last of these gradually takes over until within 2–3 years it dominates the community, tending to competitively exclude the early and mid-successional species. *G. canaliculata* then persists unless there is a further disturbance. Sousa found that algal species richness was lowest on the frequently (F) disturbed small boulders – these were dominated most often by *Ulva*. The highest levels of species richness were consistently recorded on the intermediate boulder class (I), most of which held mixtures of 3–5 abundant species from all successional stages. Finally, species richness on the rarely disturbed (R), largest boulders was lower than the intermediate class, with a monoculture of *G. canaliculata* on some of them (Figure 10.11a).

. . . and from studies of invertebrates in small streams and plankton in lakes

Disturbances in small streams often take the form of bed movements during periods of high discharge, and because of differences in flow regimes and in the substrata of stream beds, some stream communities are disturbed more frequently than others. This variation was assessed in 54 stream sites in the Taieri River in New Zealand. The pattern of richness of macroinvertebrate species conformed to the intermediate disturbance hypothesis (Figure 10.11b). Finally, in controlled field experiments, natural phytoplankton communities in Lake Plußsee (north



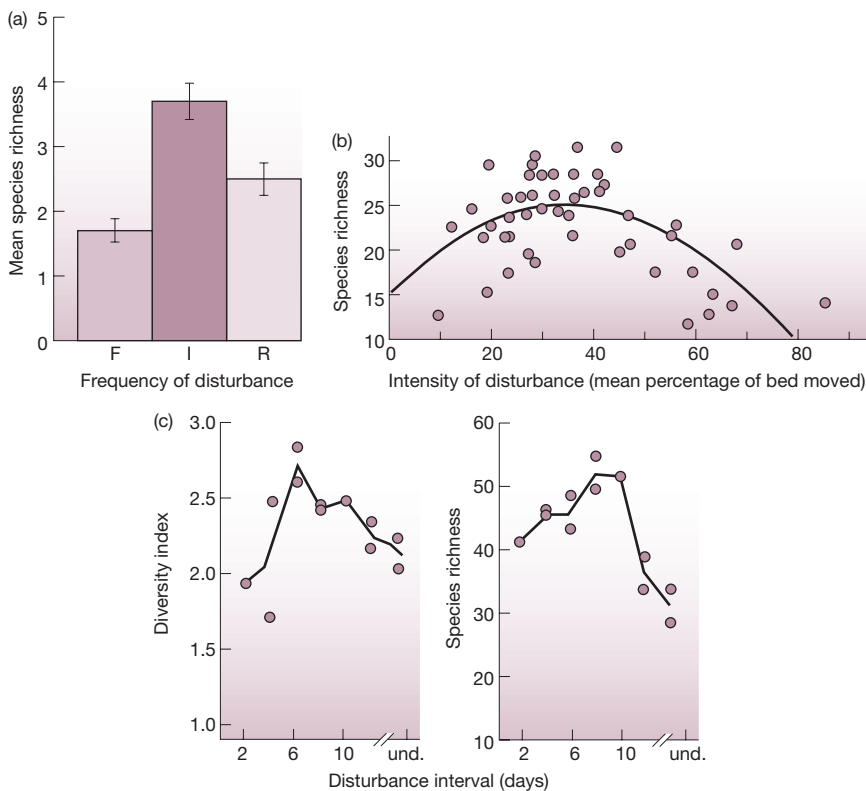


Figure 10.11

(a) Pattern in species richness ( $\pm$  SE) on rocky-shore boulders in each of three classes categorized according to the frequency with which they are disturbed: frequently disturbed (F), disturbed at an intermediate rate (I), and rarely disturbed (R). Species richness is highest at the intermediate level of disturbance. (b) Relationship between insect species richness and the intensity of disturbance, measured as the average percentage of the bed that moves during successive 2-month periods, in each of 54 stream sites in the Taieri River, New Zealand. Species richness is again highest at intermediate levels of disturbance. (c) Both species diversity (Shannon index) and species richness of phytoplankton communities are highest at intermediate frequencies of disturbance in controlled field experiments in Lake Plußsee in north Germany. 'und' represents species richness in the undisturbed state.

Germany) were disturbed at intervals of 2–12 days by disrupting the normal stratification in the water column with bubbles of compressed air. Again, both species richness and Shannon's diversity index were highest at intermediate frequencies of disturbance (Figure 10.11c).

### 10.4.3 Environmental age: evolutionary time

It has also often been suggested that communities that are 'disturbed' only on very extended time scales may nonetheless lack species because they have yet to reach an ecological or an evolutionary equilibrium. Thus communities may differ in species richness because some are closer to equilibrium and are therefore more saturated than others (see Figure 10.3d).

For example, many have argued that the tropics are richer in species than temperate regions at least in part because the tropics have existed over long and uninterrupted periods of evolutionary time, whereas the temperate regions are still recovering from the Pleistocene glaciations when temperate biotic zones shifted in the direction of the tropics. It now seems, however, that tropical areas were also disturbed during the ice ages, not directly by ice but by associated climatic changes that saw tropical forest contracting to a limited number of small refuges surrounded by grassland. Thus, although it seems likely that some communities, by virtue of disturbances in their distant past, are less saturated than others, we cannot pinpoint these communities with confidence.



An alternative explanation for lower species richness in temperate than tropical areas invokes the idea that species evolve faster in the tropics because of higher rates of mutation in these warmer climates. Wright et al. (2006) compared the rates of evolution of pairs of woody plant species, one each from tropical areas (e.g. *Eucalyptus deglupta*, *Clematis javana*, *Banksia dentate* and 42 others) and temperate areas (*Eucalyptus coccifera*, *Clematis paniculata*, *Banksia marginata*, etc., respectively). Evolution, as assessed by the rate of nucleotide substitution in a particular region of DNA, turns out to be more than twice as fast in the tropical species.

## 10.5 Gradients of species richness

Sections 10.3 and 10.4 have demonstrated how difficult explanations for variations in species richness are to formulate and test. It is easier to describe patterns, especially gradients, in species richness. These are discussed next. Explanations for these, too, however, are often very uncertain.

### 10.5.1 Habitat area and remoteness: island biogeography

It is well established that the number of species on islands decreases as island area decreases. Such a *species–area relationship* is shown in Figure 10.12a for plants on small islands east of Stockholm, Sweden.

‘Islands’, however, need not be islands of land in a sea of water. Lakes are islands in a ‘sea’ of land, mountaintops are high-altitude islands in a low-altitude ocean, gaps in a forest canopy where a tree has fallen are islands in a sea of trees,

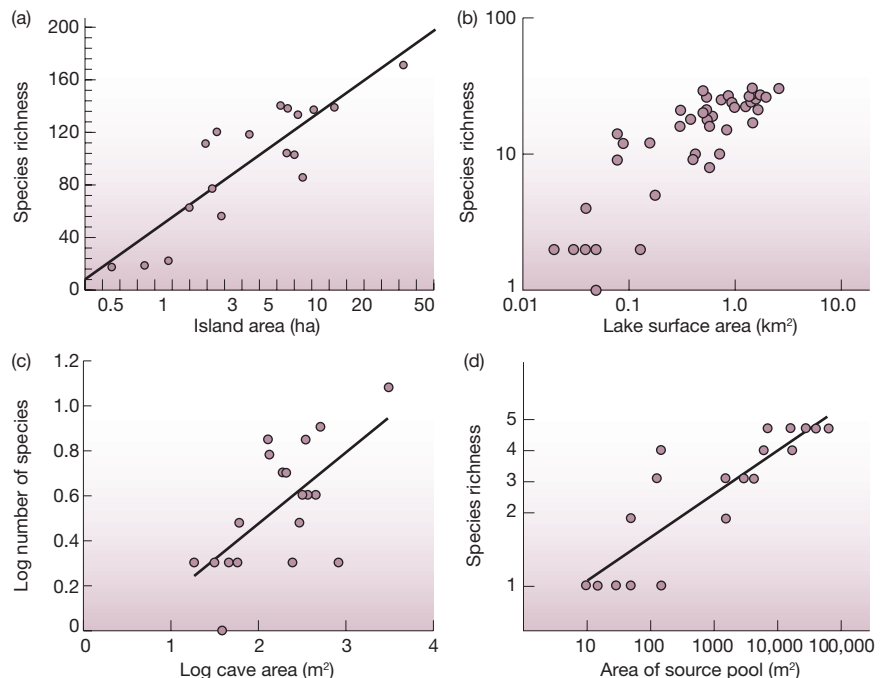
species–area relationships on oceanic islands

habitat islands and areas of mainland

**Figure 10.12**

Species–area relationships: in each case the number of species increases with ‘island’ area. (a) For plants on small islands off the east coast of Sweden in 1999. (b) For birds inhabiting lakes (‘islands’ of water in a ‘sea’ of land) in Florida. (c) For bats inhabiting different-sized caves in Mexico. (d) For fish living in Australian desert springs connected to pools of different sizes. All regression lines are significant at  $P < 0.05$ ; no line is shown in (b) because the regression is not significant.

(a) AFTER LOFGREN & JERLING, 2002; (b) AFTER HOYER & CANFIELD, 1994; (c) AFTER BRUNET & MEDELLIN, 2001; (d) AFTER KODRIC-BROWN & BROWN, 1993



and there can be islands of particular geological types, soil types or vegetation types surrounded by dissimilar types of rock, soil or vegetation. Species–area relationships can be equally apparent for these types of islands (Figure 10.12b–d).

The relationship between species richness and habitat area is one of the most consistent of all ecological patterns. However, the pattern raises an important question: ‘Is the impoverishment of species on islands more than would be expected in comparably small areas of mainland?’ In other words, does the characteristic isolation of islands contribute to their impoverishment of species? These are important questions for an understanding of community structure since there are many oceanic islands, many lakes, many mountaintops, many woodlands surrounded by fields, many isolated trees and so on.

Probably the most obvious reason why larger areas should contain more species is that larger areas typically encompass more different types of habitat. However, MacArthur and Wilson (1967) believed this explanation to be too simple. In their *equilibrium theory of island biogeography* they argued that island size and isolation themselves played important roles: that the number of species on an island is determined by a balance between immigration and extinction; that this balance is dynamic, with species continually going extinct and being replaced (through immigration) by the same or by different species; and that immigration and extinction rates may vary with island size and isolation (Box 10.3).

‘island effects’ and community structure



## 10.3 Historical landmarks

### MacArthur and Wilson’s equilibrium theory of island biogeography

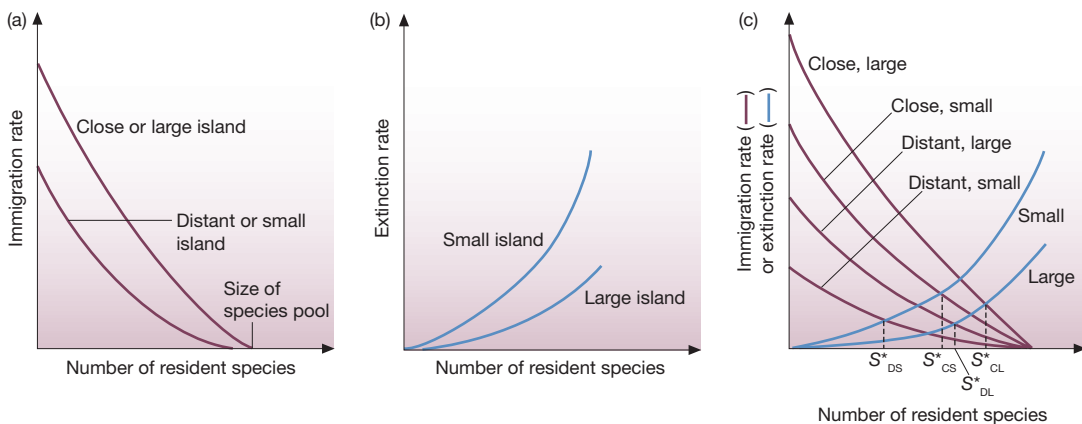
Taking immigration first, imagine an island that as yet contains no species at all. The rate of immigration of *species* will be high, because any colonizing individual represents a species new to that island. However, as the number of resident species rises, the rate of immigration of new, unrepresented species diminishes. The immigration rate reaches zero when all species from the source pool (i.e. from the mainland or from other nearby islands) are present on the island in question (Figure 10.13a).

The immigration graph is drawn as a curve, because immigration rate is likely to be particularly high when there are low numbers of residents and many of the species with the greatest powers of dispersal are yet to arrive. In fact, the curve should really be a blur rather than a single line, since the precise curve will depend on the exact sequence in which species arrive, and this will vary by chance. In this

sense, the immigration curve can be thought of as the ‘*most probable*’ curve.

The exact immigration curve will depend on the degree of remoteness of the island from its pool of potential colonizers (Figure 10.13a). The curve will always reach zero at the same point (when all members of the pool are resident), but it will generally have higher values on islands close to the source of immigration than on more remote islands, since colonizers have a greater chance of reaching an island the closer it is to the source. It is also likely that immigration rates will generally be higher on a large island than on a small island, since the larger island represents a larger ‘target’ for the colonizers (Figure 10.13a).

The rate of species extinction on an island (Figure 10.13b) is bound to be zero when there are no species there, and it will generally be low when there are few species. However, as the number of resident



**Figure 10.13**

MacArthur and Wilson's (1967) equilibrium theory of island biogeography. (a) The rate of species immigration on to an island, plotted against the number of resident species on the island, for large and small islands and for close and distant islands. (b) The rate of species extinction on an island, plotted against the number of resident species on the island for large and small islands. (c) The balance between immigration and extinction on small and large islands and on close and distant islands. In each case,  $S^*$  is the equilibrium species richness; C, close; D, distant; L, large; S, small.

species rises, the extinction rate is assumed by the theory to increase, probably at a more than proportionate rate. This is thought to occur because with more species, competitive exclusion becomes more likely, and the population size of each species is on average smaller, making it more vulnerable to chance extinction. Similar reasoning suggests that extinction rates should be higher on small than on large islands – population sizes will typically be smaller on small islands (Figure 10.13b). As with immigration, the extinction curves are best seen as 'most probable' curves.

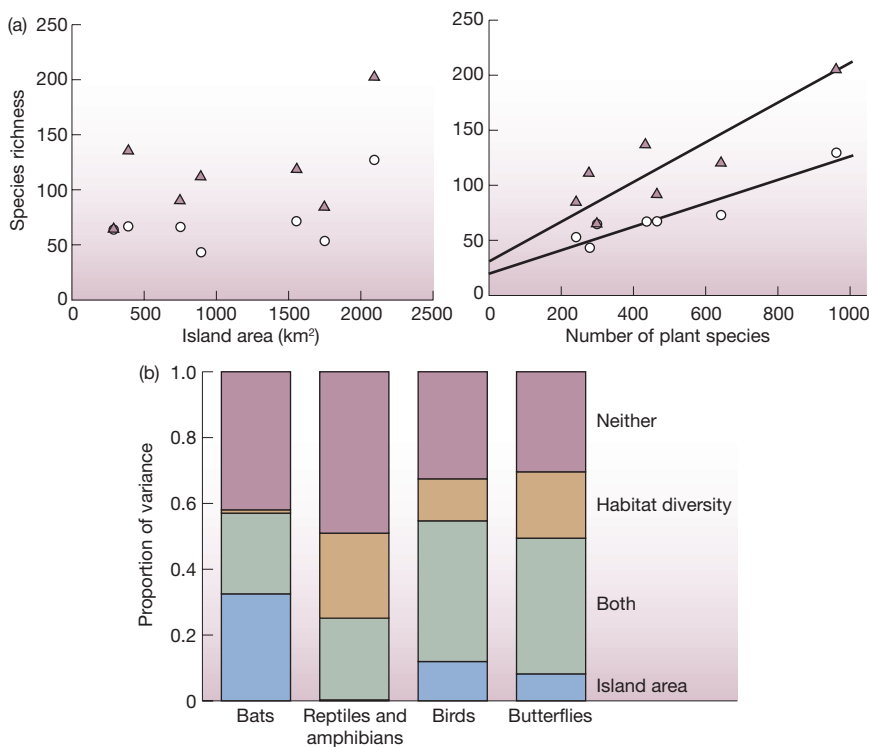
In order to see the net effect of immigration and extinction, their two curves can be superimposed (Figure 10.13c). The number of species where the curves cross ( $S^*$ ) is a dynamic equilibrium and should be the characteristic species richness for the island in question. Below  $S^*$ , richness increases (immigration rate exceeds extinction rate); above  $S^*$ , richness decreases (extinction exceeds immigration). The theory, then, makes a number of predictions, described in the text.

MacArthur and Wilson's theory makes several predictions:

- 1 The number of species on an island should eventually become roughly constant through time.
- 2 This should be a result of a continual *turnover* of species, with some becoming extinct and others immigrating.
- 3 Large islands should support more species than small islands.
- 4 Species number should decline with the increasing remoteness of an island.

partitioning variation between  
habitat diversity and area itself

On the other hand, a higher richness on larger islands would be expected simply as a consequence of larger islands having more habitat types. Does richness increase with area at a rate *greater* than could be accounted for by increases in habitat

**Figure 10.14**

(a) The relationships between species richness of herbivorous (circles) and carnivorous (triangles) beetles of the Canary Islands and both island area (left) and plant species richness (right). (b) Proportion of variance in species richness, for four animal groups, among islands in the Lesser Antilles related uniquely to island area (blue), related uniquely to habitat diversity (orange), related to correlated variation between area and habitat diversity (green) and unexplained by either (maroon). Regression lines are significant at  $P < 0.05$ ; no lines are shown in the left panel of (a) because the regression are not significant.

diversity alone? Some studies have attempted to partition species–area variation on islands into that which can be entirely accounted for in terms of habitat diversity, and that which remains and must be accounted for by island area in its own right. For beetles on the Canary Islands, the relationship between species richness and habitat diversity (as measured by plant species richness) is much stronger than that with island area, and this is particularly marked for the herbivorous beetles, presumably because of their particular food plant requirements (Figure 10.14a).

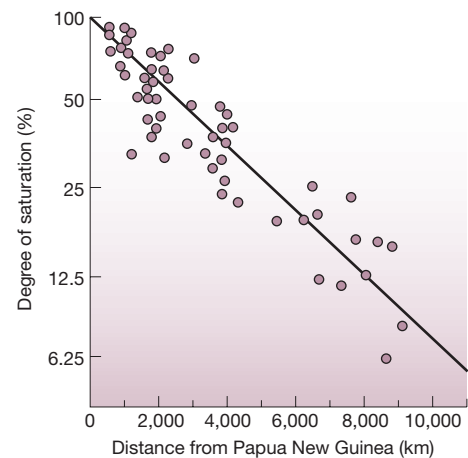
Contrasting with the Canary Island results, in a study of a variety of animal groups living on the Lesser Antilles islands in the West Indies, the variation in species richness from island to island was partitioned, statistically, into that attributable to island area alone, that attributable to habitat diversity alone, that attributable to correlated variation between area and habitat diversity (and hence not attributable to either alone) and that attributable to neither (Figure 10.14b). For reptiles and amphibians, like the beetles of the Canary Islands, habitat diversity was far more important than island area. But for bats, the reverse was the case; and for birds and butterflies, both area itself and habitat diversity had important roles to play. Overall, therefore, studies like this suggest a separate area effect (larger islands are larger targets for colonization; populations on larger islands have a lower risk of extinction) beyond a simple correlation between area and habitat diversity.

An example of species impoverishment on more remote islands can be seen in Figure 10.15 for non-marine, lowland birds on tropical islands in the southwest Pacific. With increasing distance from the large ‘source’ landmass of Papua New Guinea, there is a decline in the number of species, expressed as a percentage of the number present on an island of similar area but close to Papua New Guinea.

bird species richness on Pacific islands decreases with remoteness

**Figure 10.15**

The number of resident, non-marine, lowland bird species on islands more than 500 km from the large 'source' landmass of Papua New Guinea expressed as a percentage of the number of species on an island of equivalent area but close to Papua New Guinea – this can be thought of as the 'degree of saturation' of the bird community. It is plotted against island distance from Papua New Guinea.



AFTER DIAMOND, 1972

species missing because of insufficient time for colonization

A more transient but nonetheless important reason for the species impoverishment of islands, especially remote islands, is the fact that many lack species that they could potentially support, simply because there has been insufficient time for the species to colonize. An example is the island of Surtsey, which emerged in 1963 as a result of a volcanic eruption. The new island, 40 km southwest of Iceland, was reached by bacteria and fungi, some sea birds, a fly and seeds of several beach plants within 6 months of the start of the eruption. Its first established vascular plant was recorded in 1965, the first moss colony in 1967 and the first bush (a dwarf willow, *Salix herbacea*) in 1998. An earthworm was found in 1993 and slugs in 1998, probably carried in by birds (Hermannsson, 2000). By 2004, more than 50 species of vascular plant, 53 mosses, 45 lichens and 300 species of invertebrate had been recorded, though not all persisted (Surtsey Research Society, website [www.surtsey.is](http://www.surtsey.is)). Colonization by new species occurred both above and below the water line, with marine invertebrates, which disperse as larval stages in the ocean, accumulating faster than terrestrial plants (Figure 10.16).

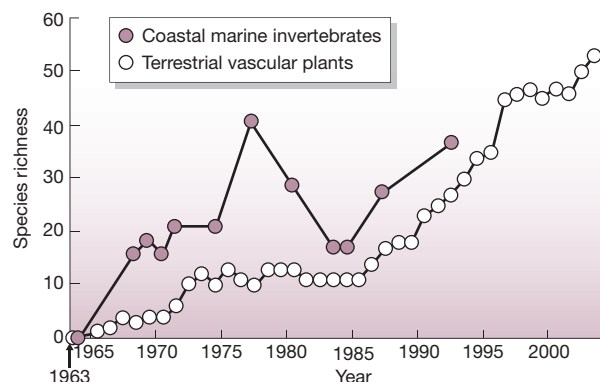
evolution rates on islands may be faster than colonization rates

Finally, it is important to reiterate that no aspect of ecology can be fully understood without reference to evolutionary processes (see Chapter 2), and this is particularly true for an understanding of island communities. On isolated islands,

**Figure 10.16.**

Regular surveys of species richness of animals and plants have occurred since the emergence in 1963 of the volcanic Surtsey Island, near Iceland. Shown here are the results of standard surveys of coastal marine invertebrates up to 1992 (barnacles, isopods, decapods, mollusks, starfish, brittlestars, sea urchins and sea squirts; maroon circles) and of terrestrial vascular plants up to 2004 (open circles).

AFTER HERMANNSSON, 2000; SURTSEY RESEARCH SOCIETY, WEBSITE [WWW.SURTSEY.IS](http://WWW.SURTSEY.IS)

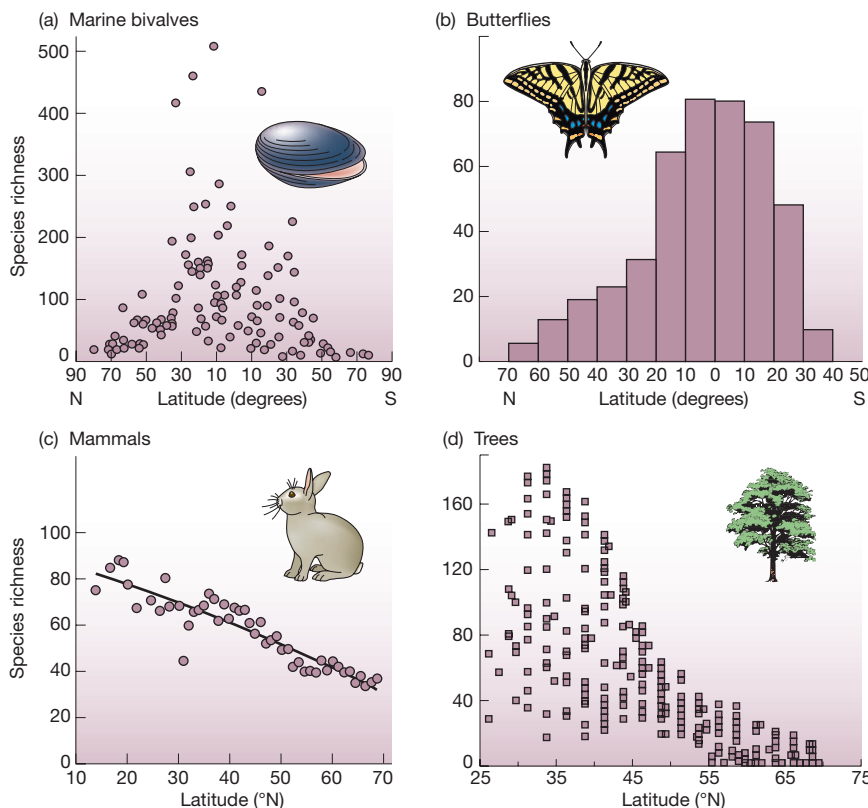


the rate at which new species evolve may be comparable to or even faster than the rate at which they arrive as new colonists. Clearly, the communities of these islands will be incompletely understood by reference only to ecological processes. Take the remarkable numbers of *Drosophila* species (fruitflies) found on the remote volcanic islands of Hawaii. There are probably about 1500 *Drosophila* species worldwide but at least 500 of these are found on the Hawaiian Islands; they have evolved, almost entirely, on the islands themselves. The communities of which they are a part are clearly much more strongly affected by local evolution and speciation than by the processes of invasion and extinction.

### 10.5.2 Latitudinal gradients

One of the most widely recognized patterns in species richness is the increase that occurs from the poles to the tropics. This can be seen in a wide variety of groups, including trees, marine invertebrates, butterflies and lizards (Figure 10.17). The pattern can be seen, moreover, in terrestrial, marine and freshwater habitats.

A number of explanations have been put forward for the general latitudinal trend in species richness, but not one of these is without problems. In the first place, the richness of tropical communities has been attributed to a greater intensity of predation and to more specialized predators. More intense predation could reduce the importance of competition, permitting greater niche overlap and promoting higher richness (see Figure 10.3c), but predation cannot readily be forwarded as



**Figure 10.17**

Latitudinal patterns in species richness for: (a) marine bivalves, (b) swallowtail butterflies, (c) mammals in North America, and (d) trees in North America. In each case there is a decline from low latitudes (the equator is at 0°) to high latitudes (the poles are at 90°).

(a) AFTER FLESSA & JABLONSKI, 1995; (b) AFTER SUTTON & COLLINS, 1991; (c) AFTER ROSENZWEIG & SANDLIN, 1997; (d) AFTER CURRIE & PAQUIN, 1987

productivity as an explanation?

the root cause of tropical richness, since this begs the question of what gives rise to the richness of the predators themselves.

Second, increasing species richness may be related to an increase in productivity as one moves from the poles to the equator. Certainly, on average, there is more heat and more light energy in increasingly tropical regions, and, as discussed in Section 10.3.1, both of these have tended to be associated with greater species richness, though increased productivity in at least some cases has been associated with reduced richness.

Moreover, light and heat are not the only determinants of plant productivity. Tropical soils tend, on average, to have lower concentrations of plant nutrients than temperate soils. The species-rich tropics might therefore be seen, in this sense, as reflecting their *low* productivity. In fact, tropical soils are poor in nutrients because most of the nutrients are locked up in the large tropical biomass. A productivity argument might therefore have to run as follows. The light, temperature and water regimes of the tropics lead to high biomass communities but not necessarily to diverse communities. This, though, leads to nutrient-poor soils and perhaps a wide range of light regimes from the forest floor to canopy far above. These in turn lead to high plant species richness and thus to high animal species richness. There is certainly no *simple* ‘productivity explanation’ for the latitudinal trend in richness.

climatic variation or evolutionary age as explanations?

Some ecologists have invoked the climate of low latitudes as a reason for their high species richness. Specifically, equatorial regions are generally less seasonal than temperate regions, and this may allow species to be more specialized (i.e. have narrower niches, see Figure 10.3b). The greater evolutionary ‘age’ of the tropics has also been proposed as a reason for their greater species richness, and another line of argument suggests that the repeated fragmentation and coalescence of tropical forest refugia promoted genetic differentiation and speciation, accounting for much of the high richness in tropical regions. And in a related context, we have already noted that the rate of evolution may be faster in the tropics (see Section 10.4.3). All these ideas are plausible too, but far from proven generalizations.

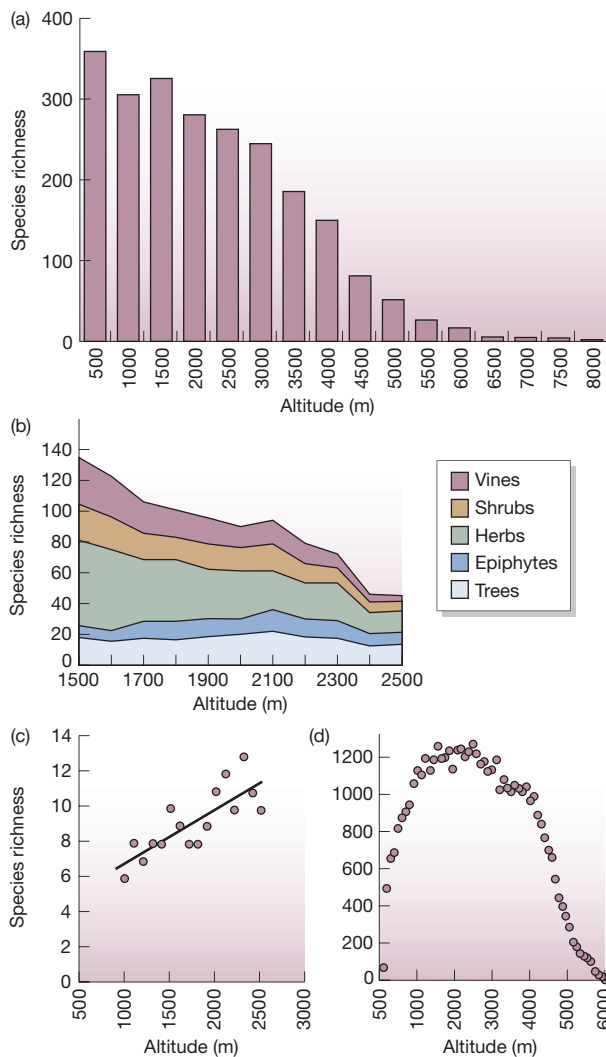
Overall, therefore, the latitudinal gradient lacks an unambiguous explanation. This is hardly surprising. The components of a possible explanation – trends with productivity, climatic stability and so on – are themselves understood only in an incomplete and rudimentary way, and the latitudinal gradient intertwines these components with one another, and with other, often opposing forces – isolation, harshness and so on.

### 10.5.3 Gradients with altitude and depth

A decrease in species richness with altitude, analogous to that observed with latitude, has frequently been reported in terrestrial environments (e.g. Figure 10.18a, b). On the other hand, some have reported an increase with altitude (e.g. Figure 10.18c), while about half the studies of altitudinal species richness have described hump-shaped patterns (e.g. Figure 10.18d) (Rahbek, 1995).

At least some of the factors instrumental in the latitudinal trend in richness are also likely to be important as explanations for altitudinal trends (though the problems in explaining the latitudinal trend apply equally to altitude). For example, declines in species richness have often been explained in terms of decreasing productivity associated with lower temperatures and shorter growing seasons at higher altitude, or physiological stress associated with climatic extremes near



**Figure 10.18**

Relationships between species richness and altitude for: (a) breeding birds in the Nepalese Himalayas, (b) plants in the Sierra Manantlán, Mexico, (c) ants in Lee Canyon in the Spring Mountains of Nevada, USA, and (d) flowering plants in the Nepalese Himalayas. Species richness decreases with altitude in (a) and (b), increases with altitude in (c) and shows a hump-backed relationship in (d).

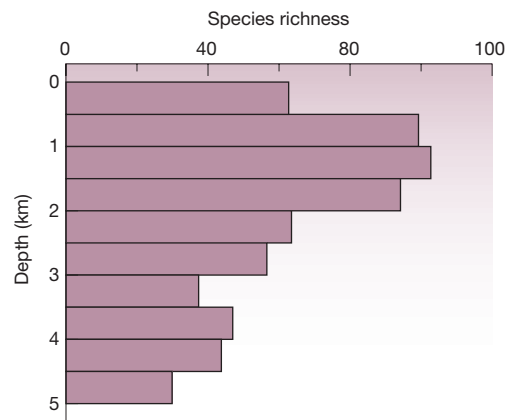
(a) AFTER HUNTER & YONZON, 1982; (b) AFTER VÁZQUEZ & GIVINSH, 1988; (c) AFTER SANDERS ET AL., 2003; (d) AFTER GRITNES & VETÅS, 2002

mountaintops. Indeed, the explanation for the converse, positive relationship between ant diversity and altitude in Figure 10.18c, is that precipitation increased with altitude in this case, resulting in higher productivity and less physiologically extreme conditions at higher altitude. In addition, high-altitude communities almost invariably occupy smaller areas than lowlands at equivalent latitudes, and they will usually be more isolated from similar communities than lowland sites. Therefore the effects of area and isolation are likely to contribute to observed decreases in species richness with altitude.

In aquatic environments, the change in species richness with depth shows some strong similarities to the terrestrial gradient with altitude. In larger lakes, the cold, dark, oxygen-poor abyssal depths contain fewer species than the shallow surface waters. Likewise, in marine habitats, plants are confined to the photic zone (where light penetrates and they can photosynthesize), which rarely extends below 30 m. In the open ocean, therefore, there is a rapid decrease in richness

**Figure 10.19**

Depth gradient in species richness of bottom-dwelling vertebrates and invertebrates (fish, decapods, holothurians, asteroids) in the ocean southwest of Ireland.



AFTER ANGEL 1994

with depth, reversed only by the variety of bizarre animals living on the ocean floor. Interestingly, however, in coastal regions the effect of depth on the species richness of benthic (bottom-dwelling) animals is to produce not a single gradient, but a peak of richness at about 1000 m, possibly reflecting higher environmental predictability there (Figure 10.19). At greater depths, beyond the continental slope, species richness declines again, probably because of the extreme paucity of food resources in abyssal regions.

### 10.5.4 Gradients during community succession

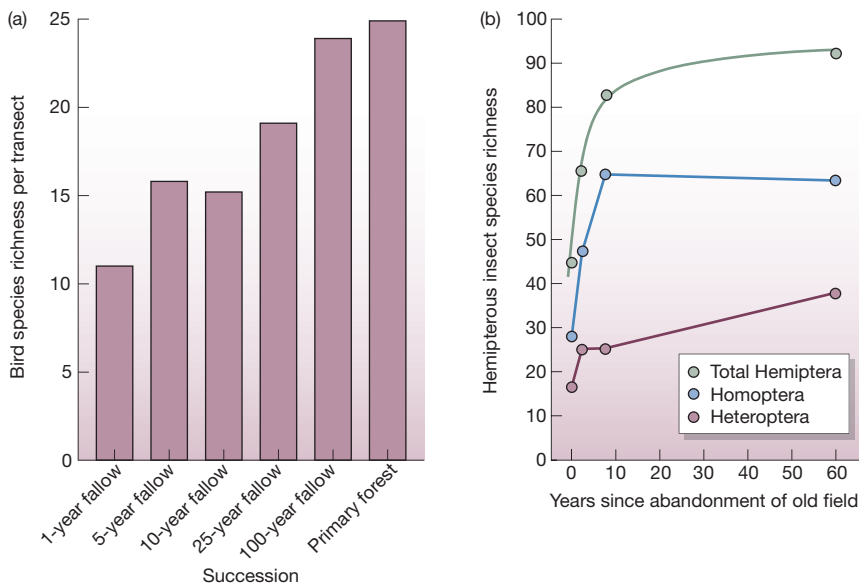
Section 9.4 described how, in community successions, if they run their full course, the number of species first increases (because of colonization) but eventually decreases (because of competition). This is most firmly established for plants, but the few studies that have been carried out on animals in successions indicate, at the least, a parallel increase in species richness in the early stages of succession. Figure 10.20 illustrates this for birds following the cessation of shifting cultivation in tropical rain forest, and for insects associated with an old-field succession in a temperate region.

To a certain extent, the successional gradient is a necessary consequence of the gradual colonization of an area by species from surrounding communities that are at later successional stages; that is, later stages are more fully saturated with species (see Figure 10.3d). However, this is a small part of the story, since succession involves a process of the replacement of species and not just the mere addition of new ones.

a cascade effect?

Indeed, as with the other gradients in species richness, there is something of a cascade effect with succession: one process that increases richness kick-starts a second, which feeds into a third, and so on. The earliest species will be those that are the best colonizers and the best competitors for open space. They immediately provide resources (and introduce heterogeneity) that were not previously present. For example, the earliest plants generate resource depletion zones (see Section 3.3.2) in the soil that inevitably increase the spatial heterogeneity of plant nutrients. The plants themselves provide a new variety of microhabitats, and for the animals that might feed on them they provide a much greater range of food resources (see Figure 10.3a). The increase in herbivory and predation may then

(a) AFTER SHANKAR RAMANI ET AL., 1998; (b) AFTER BROWN & SOUTHWOOD, 1983



**Figure 10.20**

Examples of increases in animal species richness during succession. (a) Bird species richness increased after shifting cultivation ceased in tropical rain forest in northeast India. Areas that were left fallow after being retired from cultivation for known periods were compared with the undisturbed primary forest. (b) The species richness of true bugs (insects in the suborders Homoptera and Heteroptera of the order Hemiptera) increased with time after an English farm field was taken out of cultivation.

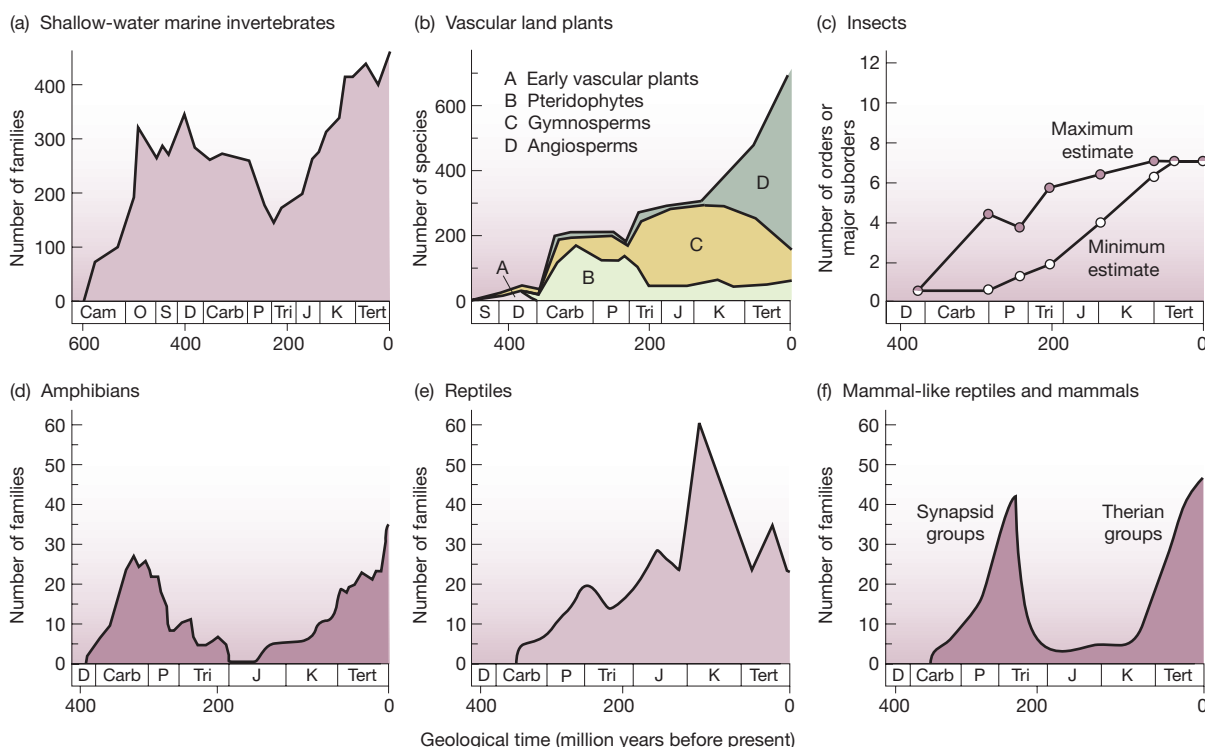
feed back to promote further increases in species richness (predator-mediated coexistence, Figure 10.3c), which provides further resources and more heterogeneity, and so on. In addition, temperature, humidity and wind speed show much less temporal variation within a forest than in an exposed early successional stage, and the enhanced constancy of the environment may provide a stability of conditions and resources that permits specialist species to build up populations and persist (Figure 10.3b). As with the other gradients, the interaction of many factors makes it difficult to disentangle cause from effect. But with the successional gradient of richness, the tangled web of cause and effect appears to be of the essence.

## 10.6 Patterns in taxon richness in the fossil record

Finally, it is of interest to take the processes that are believed to be instrumental in generating present-day gradients in richness and apply them to trends occurring over much longer timespans. The imperfection of the fossil record has always been the greatest impediment to the paleontological study of evolution. Nevertheless, some general patterns have emerged, and our knowledge of six important groups of organisms is summarized in Figure 10.21.

Until about 600 million years ago, the world was populated virtually only by bacteria and algae, but then almost all the phyla of marine invertebrates entered the fossil record within the space of only a few million years (Figure 10.21a). We have seen that the introduction of a higher trophic level can increase richness at a lower level by ‘exploiter-mediated coexistence’; thus, it can be argued that the first single-celled herbivorous protist was probably instrumental in the Cambrian explosion in species richness. The opening up of space by grazing on the algal monoculture, coupled with the availability of recently evolved eukaryotic cells, may have caused the biggest burst of evolutionary diversification in the planet’s history.

the Cambrian explosion:  
exploiter-mediated coexistence?



**Figure 10.21**

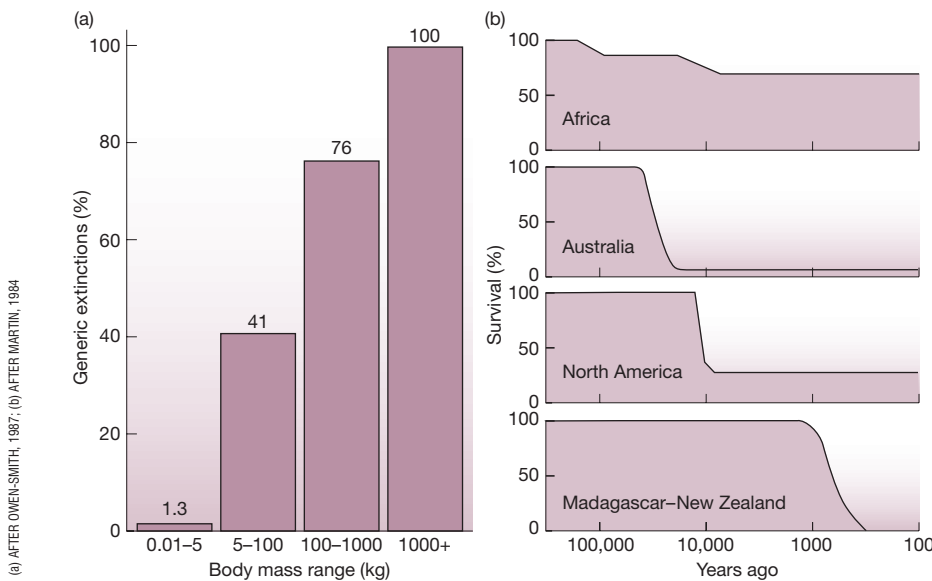
Patterns in taxon richness through the fossil record. (a) Families of shallow-water marine invertebrates. (b) Species of vascular land plants in four groups – early vascular plants, pteridophytes, gymnosperms and angiosperms. (c) Orders and major suborders of insects (minimum values are derived from definite fossil records; the maximum values include 'possible' records). (d) Families of amphibians, (e) families of reptiles and (f) families of 'mammal-like reptiles' (Synapsids) and Therian mammals (includes both marsupial and placental groups). Key to geological periods: Cam, Cambrian; O, Ordovician; S, Silurian; D, Devonian; Carb, Carboniferous; P, Permian; Tri, Triassic; J, Jurassic; K, Cretaceous; Tert, Tertiary.

the Permian decline: a species–area relationship?

In contrast, the equally dramatic decline in the number of families of shallow-water invertebrates at the end of the Permian (Figure 10.21a) could have been a result of the coalescence of the Earth's continents to produce the single supercontinent of Pangaea; the joining of continents produced a marked reduction in the area occupied by shallow seas (which occur around the periphery of continents) and thus a marked decline in the area of habitat available to shallow-water invertebrates. Moreover, at this time the world was subject to a prolonged period of global cooling in which huge quantities of water were locked up in enlarged polar caps and glaciers, causing a widespread reduction of warm, shallow sea environments. Thus, a species–area relationship may be invoked to account for a reduction in taxon richness at this time.

competitive displacement among the major plant groups?

The analysis of fossil remains of vascular land plants (Figure 10.21b) reveals four distinct evolutionary phases: (i) a Silurian–mid-Devonian proliferation of early vascular plants; (ii) a subsequent late-Devonian–Carboniferous radiation of fern-like lineages (pteridophytes); (iii) the appearance of seed plants in the late Devonian and the adaptive radiation to a gymnosperm-dominated flora; and (iv) the appearance and rise of flowering plants (angiosperms) in the Cretaceous and Tertiary. It seems that after initial invasion of the land, made possible by

**Figure 10.22**

(a) The percentage of genera of large mammalian herbivores that have gone extinct in the last 130,000 years is strongly size-dependent (data from North and South America, Europe and Australia combined). (b) Percentage survival of large animals on three continents and two large islands (New Zealand and Madagascar). The dramatic declines in taxon richness in Australia, North America and the islands of New Zealand and Madagascar occurred at different times in history.

the appearance of roots, the diversification of each plant group coincided with a decline in species numbers of the previously dominant group. In two of the transitions (early plants to gymnosperms, and gymnosperms to angiosperms), this pattern may reflect the competitive displacement of older, less specialized taxa by newer and presumably more specialized taxa.

The first undoubtedly herbivorous insects are known from the Carboniferous. Thereafter, modern orders appeared steadily (Figure 10.21c) with the Lepidoptera (butterflies and moths) arriving last on the scene, at the same time as the rise of the angiosperms. Coevolution between plants and herbivorous insects (see Section 8.4.3) has almost certainly been, and still is, an important mechanism driving the increase in richness observed in both land plants and insects through their evolution.

Toward the end of the last ice age, the continents were much richer in large animals than they are today. For example, Australia was home to many genera of giant marsupials; North America had its mammoths, giant ground sloths and more than 70 other genera of large mammals; and New Zealand and Madagascar were home to giant flightless birds, the moas (*Dinornithidae*) and elephant birds (*Aepyornithidae*), respectively. During the past 30,000 years or so, a major loss of this biotic diversity has occurred over much of the globe. The extinctions particularly affected large terrestrial animals (Figure 10.22a), they were more pronounced in some parts of the world than others, and they occurred at different times in different places (Figure 10.22b). The extinctions mirror patterns of human migration. Thus, the arrival in Australia of ancestral aborigines occurred between 40,000 and 30,000 years ago; stone spear points became abundant throughout the United States about 11,500 years ago; and humans have been in both Madagascar and New Zealand for 1000 years. It can be convincingly argued, therefore, that the arrival of efficient human hunters led to the rapid overexploitation of vulnerable and profitable large prey. Africa, where humans originated, shows much less evidence of loss, perhaps because coevolution of

extinctions of large animals in the Pleistocene: prehistoric overkill?

large animals alongside early humans provided ample time for them to develop effective defenses (Owen-Smith, 1987).

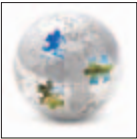
The Pleistocene extinctions herald the modern age, in which the influence upon natural communities of human activities has been increasing dramatically.

## 10.7 Appraisal of patterns in species richness

richness patterns –  
generalizations and exceptions

There are many generalizations that can be made about the species richness of communities. We have seen how richness may peak at intermediate levels of available environmental energy or of disturbance frequency, and how richness declines with a reduction in island area or an increase in island remoteness. We find also that species richness decreases with increasing latitude, and declines or shows a hump-backed relationship with altitude or depth in the ocean. It increases with an increase in spatial heterogeneity but may decrease with an increase in temporal heterogeneity (increased climatic variation). It increases, at least initially, during the course of succession and with the passage of evolutionary time. However, for many of these generalizations important exceptions can be found, and for most of them the current explanations are not entirely adequate.

It also needs to be recognized that global patterns of species richness have been disrupted in dramatic ways by human activities, such as land-use development, pollution and the introduction of exotic species (Box 10.4).



## 10.4 TOPICAL ECOncerns

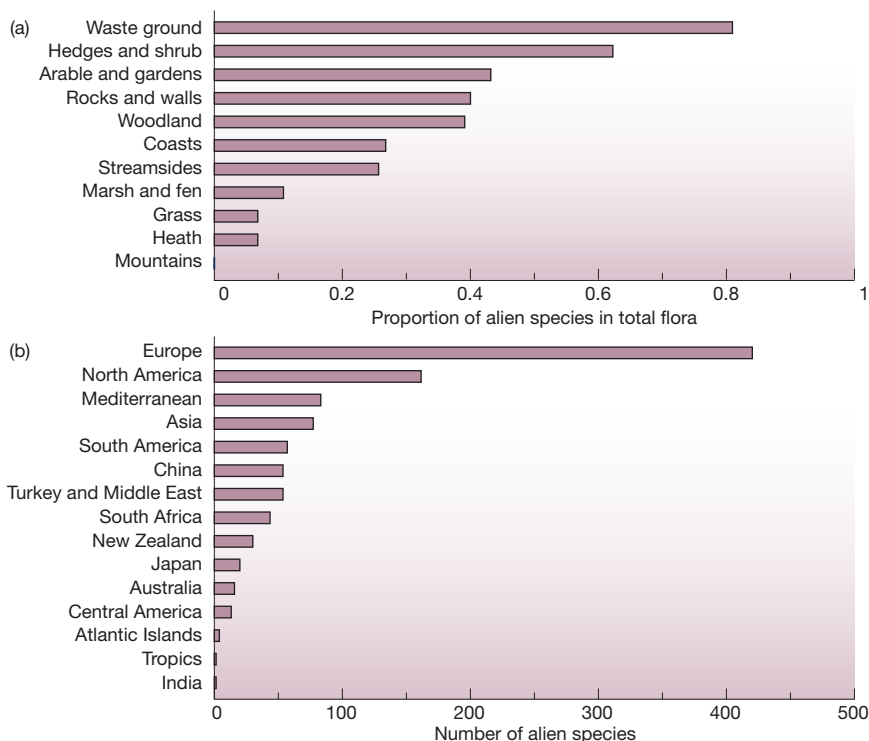
### The flood of exotic species

Throughout the history of the world, species have invaded new geographic areas, as a result of chance colonizations (e.g. dispersed to remote areas by wind or to remote islands on floating debris; see Section 10.5.1) or during the slow northward spread of forest trees in the centuries since the last ice age (see Section 2.5). However, human activities have increased this historical trickle to a flood, disrupting global patterns of species richness.

Some human-caused introductions are an accidental consequence of human transport. Other species have been introduced intentionally, perhaps to bring a pest under control (see Section 12.5), to produce a new agricultural product or to provide new recreational opportunities. Many invaders become part of natural

communities without obvious consequences. But some have been responsible for driving native species extinct or changing natural communities in significant ways (see Section 14.2.3).

The alien plants of the British Isles illustrate a number of general points about invaders. Species inhabiting areas where people live and work are more likely to be transported to new regions, where they will tend to be deposited in habitats like those where they originated. As a result, more alien species are found in disturbed habitats close to human transport centers (docks, railways, cities) and fewer in remote mountain areas (Figure 10.23a). Moreover, more invaders to the British Isles are likely to arrive from nearby geographic locations (e.g. Europe) or



**Figure 10.23**

The alien flora of the British Isles (a) according to community type (note the large number of aliens in open, disturbed habitats close to human settlements) and (b) by geographic origin (reflecting proximity, trade and climatic similarity).

AFTER GODFRAY & CRAWLEY, 1998

from remote locations whose climate matches that of Britain (e.g. New Zealand) (Figure 10.23b). Note the small number of alien plants from tropical environments; these species usually lack the frost-hardiness required to survive the British winter.

*Review the options available to governments to prevent (or reduce the likelihood) of invasions of undesirable alien species.*

Unraveling richness patterns is one of the most difficult and challenging areas of modern ecology. Clear, unambiguous predictions and tests of ideas are often very difficult to devise and will require great ingenuity of future generations of ecologists. Because of the increasing importance of recognizing and conserving the world's biological diversity, though, it is crucial that we come to understand thoroughly these patterns in species richness. We will assess the adverse effects of human activities, and how they may be remedied, in Chapters 12–14.





## Summary

### SUMMARY

#### Richness and diversity

The number of species in a community is referred to as its species richness. Richness, though, ignores the fact that some species are rare and others common. Diversity indices are designed to combine species richness and the evenness of the distribution of individuals among those species. Attempts to describe a complex community structure by one single attribute, such as richness or diversity, can still be criticized because so much valuable information is lost. A more complete picture is therefore sometimes provided in a rank–abundance diagram.

A simple model can help us understand the determinants of species richness. Within it, a community will contain more species the greater the range of resources, if the species are more specialized in their use of resources, if species overlap to a greater extent in their use of resources, or if the community is more fully saturated.

#### Productivity and resource richness

If higher productivity is correlated with a wider range of available resources, then this is likely to lead to an increase in species richness, but more of the same might lead to more individuals per species rather than more species. In general, though, species richness often increases with the richness of available resources and productivity, although in some cases the reverse has been observed – the paradox of enrichment – and others have found species richness to be highest at intermediate levels of productivity.

#### Predation intensity

Predation can exclude certain prey species and reduce richness or permit more niche overlap and thus greater richness (predator-mediated coexistence). Overall, therefore, there may be a humped relationship between predation intensity and species richness in a community, with greatest richness at intermediate intensities.

#### Spatial heterogeneity

Environments that are more spatially heterogeneous often accommodate extra species because they provide a greater variety of microhabitats, a greater range of microclimates, more types of places to hide from predators and so on – the resource spectrum is increased.

#### Environmental harshness

Environments dominated by an extreme abiotic factor – often called harsh environments – are more difficult to recognize than might be immediately apparent. Some apparently harsh environments do support few species, but any overall association has proved extremely difficult to establish.

#### Climatic variation

In a predictable, seasonally changing environment, different species may be suited to conditions at different times of the year. More species might therefore be expected to coexist than in a completely constant environment. On the other hand, opportunities for specialization (e.g. obligate fruit-eating) exist in a non-seasonal environment that are not available in a seasonal environment. Unpredictable climatic variation (climatic instability) could decrease richness by denying species the chance to specialize, or increase richness by preventing competitive exclusion. There is no established relationship between climatic instability and species richness.

#### Disturbance

The intermediate disturbance hypothesis suggests that very frequent disturbances keep most patches at an early stage of succession (where there are few species), but very rare disturbances allow most patches to become dominated by the best competitors (where there are also few species). Originally proposed to account for patterns of richness in tropical rain forests and coral reefs, the hypothesis has

occupied a central place in the development of ecological theory.

### Environmental age: evolutionary time

It has often been suggested that communities may differ in richness because some are closer to equilibrium and therefore more saturated than others, and that the tropics are rich in species in part because the tropics have existed over long and uninterrupted periods of evolutionary time. A simplistic contrast between the unchanging tropics and the disturbed and recovering temperate regions, however, is untenable.

### Habitat area and remoteness: island biogeography

Islands need not be islands of land in a sea of water. Lakes are islands in a sea of land; mountaintops are high-altitude islands in a low-altitude ocean. The number of species on islands decreases as island area decreases, in part because larger areas typically encompass more different types of habitat. However, MacArthur and Wilson's equilibrium theory of island biogeography argues for a separate island effect based on a balance between immigration and extinction, and the theory has received much support. In addition, on isolated islands especially, the rate at which new species evolve may be comparable to or even faster than the rate at which they arrive as new colonists.

### Gradients in species richness

Richness increases from the poles to the tropics. Predation, productivity, climatic variation and the greater evolutionary age of the tropics have been put forward as partial explanations.

In terrestrial environments, richness often (but not always) decreases with altitude. Factors instrumental in the latitudinal trend are also likely to be important in this, but so are area and isolation. In aquatic environments, richness usually decreases with depth for similar reasons.

In successions, if they run their full course, richness first increases (because of colonization) but eventually decreases (because of competition). There may also be a cascade effect: one process that increases richness kick-starts a second, which feeds into a third, and so on.

### Patterns in taxon richness in the fossil record

The Cambrian explosion of taxa may have been an example of exploiter-mediated coexistence. The Permian decline may reflect a species–area relationship when the Earth's continents coalesced into Pangaea. The changing pattern of plant taxa may reflect the competitive displacement of older, less specialized taxa by newer, more specialized ones. The extinctions of many large animals in the Pleistocene may reflect the hand of human predation and hold lessons for the present day.

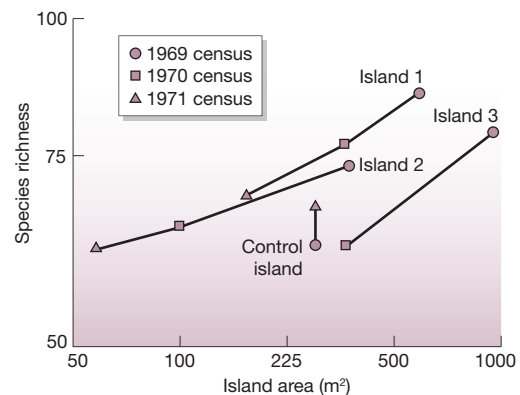
## Review questions

### REVIEW QUESTIONS

Asterisks indicate challenge questions

- 1 Explain species richness, diversity index and rank–abundance diagrams and compare what each measures.
- 2 What is the paradox of enrichment, and how can the paradox be resolved?
- 3 Explain, with examples, the contrasting effects that predation can have on species richness.
- 4\* Researchers have reported a variety of hump-shaped patterns in species richness, with peaks of richness occurring at intermediate levels of productivity, predation pressure, disturbance and depth in the ocean. Review the evidence and consider whether these patterns have any underlying mechanisms in common.
- 5 Why is it so difficult to identify 'harsh' environments?

- 6 Explain the intermediate disturbance hypothesis.
- 7 Islands need not be islands of land in an ocean of water. Compile a list of other types of habitat islands over as wide a range of spatial scales as possible.
- 8\* An experiment was carried out to try to separate the effects of habitat diversity and area on arthropod species richness on some small mangrove islands in the Bay of Florida. These consisted of pure stands of the mangrove species *Rhizophora mangle*, which support communities of insects, spiders, scorpions and isopods. After a preliminary faunal survey, some islands were reduced in size by means of a power saw and brute force! Habitat diversity was not affected, but arthropod species richness on three islands nonetheless diminished over a period of 2 years (Figure 10.24). A control island, the size of which was unchanged, showed a slight increase in richness over the same period. Which of the predictions of island biogeography theory are supported by the results in the figure? What further data would you require to test the other predictions? How would you account for the slight increase in species richness on the control island?
- 9\* A cascade effect is sometimes proposed to explain the increase in species richness



**Figure 10.24**

The effect on the number of arthropod species of artificially reducing the size of three mangrove islands. Islands 1 and 2 were reduced in size after both the 1969 and 1970 censuses. Island 3 was reduced only after the 1969 census. The control island was not reduced, and the change in its species richness was attributable to random fluctuations.

AFTER SIMBERLOFF, 1976

during a community succession. How might a similar cascade concept apply to the commonly observed gradient of species richness with latitude?

- 10 Describe how theories of species richness that have been derived on ecological time scales can also be applied to patterns observed in the fossil record.

# Chapter 11



## The flux of energy and matter through ecosystems

### *Chapter contents*

#### CHAPTER CONTENTS

- 11.1 Introduction
- 11.2 Primary productivity
- 11.3 The fate of primary productivity
- 11.4 The process of decomposition
- 11.5 The flux of matter through ecosystems
- 11.6 Global biogeochemical cycles

### *Key concepts*

#### KEY CONCEPTS

In this chapter, you will:

- recognize that communities are intimately linked with the abiotic environment by fluxes of energy and matter
- understand that net primary productivity is not evenly spread across the Earth
- appreciate that transfer of energy between trophic levels is always inefficient – secondary productivity by herbivores is approximately an order of magnitude less than the primary productivity on which it is based
- recognize that much more of a community's energy and matter passes through the decomposer system than the live consumer system
- appreciate that decomposition results in complex, energy-rich molecules being broken down by their consumers (decomposers and detritivores) into carbon dioxide, water and inorganic nutrients
- understand that in global geochemical cycles, nutrients are moved over vast distances by winds in the atmosphere and in the moving waters of streams and ocean currents

*Like all biological entities, ecological communities require matter for their construction and energy for their activities. We need to understand the routes by which matter and energy enter and leave ecosystems, how they are transformed into plant biomass and how this fuels the rest of the community – bacteria and fungi, herbivores, detritivores and their consumers.*

## 11.1 Introduction

All biological entities require matter for their construction and energy for their activities. This is true not only for individual organisms, but also for the populations and communities that they form in nature. The intrinsic importance of fluxes of energy and of matter means that community processes are particularly strongly linked with the abiotic environment. The term *ecosystem* is used to denote the biological community *together with* the abiotic environment in which it is set. Thus, ecosystems normally include primary producers, decomposers and detritivores, a pool of dead organic matter, herbivores, carnivores and parasites *plus* the physicochemical environment that provides living conditions and acts both as a source and a sink for energy and matter. It was Lindeman (1942) who laid the foundations for ecological energetics, a science with profound implications both for understanding ecosystem processes and for human food production (Box 11.1).

In order to examine ecosystem processes, it is important to understand some key terms.

the standing crop and primary and secondary productivity

- *Standing crop*. The bodies of the living organisms within a unit area constitute a standing crop of biomass.
- *Biomass*. By biomass we mean the mass of organisms per unit area of ground (or water) and this is usually expressed in units of energy (e.g. joules per square meter) or dry organic matter (e.g. tonnes per hectare). In practice we include in biomass all those parts, living or dead, that are attached to the living organism. Thus, it is conventional to regard the whole body of a tree as biomass, despite the fact that most of the wood is dead. Organisms (or their parts) cease to be regarded as biomass when they die (or are shed) and become components of dead organic matter.
- *Primary productivity*. The primary productivity of a community is the rate at which biomass is produced *per unit area* by plants, the primary producers. It can be expressed either in units of energy (e.g. joules per square meter per day) or of dry organic matter (e.g. kilograms per hectare per year).
- *Gross primary productivity*. The total fixation of energy by photosynthesis is referred to as gross primary productivity (GPP). A proportion of this, however, is respired away by the plant itself and is lost from the community as respiratory heat (R).



## 11.1 HISTORICAL LANDMARKS

### 11.1 Historical landmarks

#### Ecological energetics and the biological basis of productivity and human welfare

A classic paper by Lindeman (1942) laid the foundations of a science of ecological energetics. He attempted to quantify the concept of food chains and food webs by considering the efficiency of transfer between trophic levels – from incident radiation received by a community through its capture by green plants in photosynthesis to its subsequent use by bacteria, fungi and animals.

Lindeman's paper was a major catalyst that stimulated the International Biological Programme (IBP for short). The subject of the IBP was 'the biological basis of productivity and human welfare'. Given the problem of a rapidly increasing human population, it was recognized that scientific knowledge would be required for rational resource management. Cooperative international research programs focused on the ecological energetics of areas of land, fresh waters and the seas. The IBP provided the first occasion on which biologists throughout the world were challenged to work together towards a common end.

More recently, another pressing issue has galvanized the ecological community into action. Deforestation, the burning of fossil fuels and other human influences are causing dramatic changes to global climate and

atmospheric composition, and can be expected in turn to influence patterns of productivity and the composition of vegetation on a global scale. Among the prime objectives of the International Geosphere-Biosphere Programme (IGBP), established in the early 1990s, was to predict the effects of changes in climate and atmospheric composition on agriculture and food production. The Food and Agriculture Organization (FAO) of the United Nations reported recently that some of the predicted changes seemed to be advancing at a higher rate than anticipated, including:

- 1 A likely decline in precipitation in some food-insecure areas such as southern Africa and the northern region of Latin America.
- 2 Changes in seasonal distribution of rainfall, with less falling in the main crop-growing season.
- 3 Higher night-time temperatures, which may adversely affect grain production.
- 4 Disruption of food supply through more frequent and severe extreme weather events.

We will see in this chapter why changes to water availability and temperature, among other factors, can have such profound effects on productivity.

- *Net primary productivity.* The difference between GPP and R is known as net primary productivity (NPP) and represents the actual rate of production of new biomass that is available for consumption by heterotrophic organisms (bacteria, fungi and animals).
- *Secondary productivity.* The rate of production of biomass by heterotrophs is called secondary productivity.

A proportion of primary production is consumed by herbivores, which, in turn, are consumed by carnivores. These constitute the *live consumer system*. The fraction of NPP that is not eaten by herbivores passes through the *decomposer system*. We distinguish two groups of organisms responsible for the decomposition of dead organic matter (detritus): bacteria and fungi are called *decomposers* while animals that consume dead matter are known as *detritivores*.

live consumer systems and  
decomposer systems



## 11.2 Primary productivity

### 11.2.1 Geographic patterns in primary productivity

the open ocean is, in effect, a marine desert

The functioning of the biota of the Earth, and of the communities across the surface of the planet, depend crucially on the levels of productivity that plants are able to achieve. The total NPP of the planet is estimated to be about 105 petagrams of carbon per year ( $1 \text{ Pg} = 10^{15} \text{ g}$ ). Of this,  $56.4 \text{ Pg C yr}^{-1}$  is produced in terrestrial ecosystems and  $48.3 \text{ Pg C yr}^{-1}$  in aquatic ecosystems (Table 11.1). Thus, although oceans cover about two-thirds of the world's surface, they account for less than half of its production and most of the ocean is, in effect, a marine desert. On the land, tropical rain forests and savannas account between them for about 60% of terrestrial NPP, reflecting the large areas covered by these biomes and their high levels of productivity.

the productivity of forests, grasslands, crops and lakes follows a latitudinal pattern

In the forest biomes of the world, there is a general latitudinal trend of increasing productivity from boreal ( $1019\text{--}1034 \text{ g C m}^{-2} \text{ yr}^{-1}$ ), through temperate ( $1327\text{--}1499 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) to tropical ( $> 3000 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) forest (Falge et al., 2002). A similar latitudinal trend has been reported for tundra and grassland communities, various cultivated crops and lakes. Despite considerable variation, these general trends with latitude suggest that radiation (a resource) and temperature (a condition) may be the factors usually limiting the productivity of communities. Other factors can, however, constrain productivity within even narrower limits. In the sea, where no latitudinal trend has been reported, productivity is more often limited by a shortage of nutrients.

### 11.2.2 Factors limiting primary productivity

What, then, limits primary productivity? In terrestrial communities, solar radiation, carbon dioxide, water and soil nutrients are the resources required for primary production while temperature, a condition, has a strong influence on the

**Table 11.1**

Net primary production (NPP) per year summed for each of the major biomes and for the planet in total (in units of petagrams of carbon).

MARINE	NPP	TERRESTRIAL	NPP
Tropical and subtropical oceans	13.0	Tropical rain forests	17.8
Temperate oceans	16.3	Broadleaf deciduous forests	1.5
Polar oceans	6.4	Mixed broad/needleleaf forests	3.1
Coastal	10.7	Needleleaf evergreen forests	3.1
Salt marsh/estuaries/seaweed	1.2	Needleleaf deciduous forests	1.4
Coral reefs	0.7	Savannas	16.8
		Perennial grasslands	2.4
		Broadleaf shrubs with bare soil	1.0
		Tundra	0.8
		Desert	0.5
		Cultivation	8.0
Total	48.3	Total	56.4



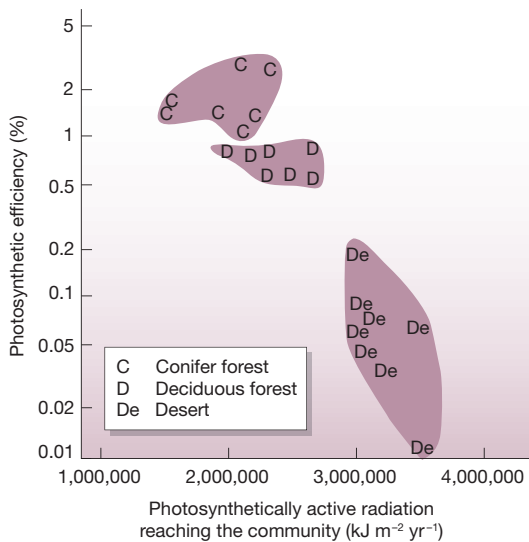


Figure 11.1

Photosynthetic efficiency (percentage of incoming photosynthetically active radiation converted to above-ground net primary production) for three sets of terrestrial communities in the United States. Desert ecosystems receive the greatest levels of radiation, but are much less efficient than forests in converting it to biomass.

AFTER WEBB ET AL., 1983

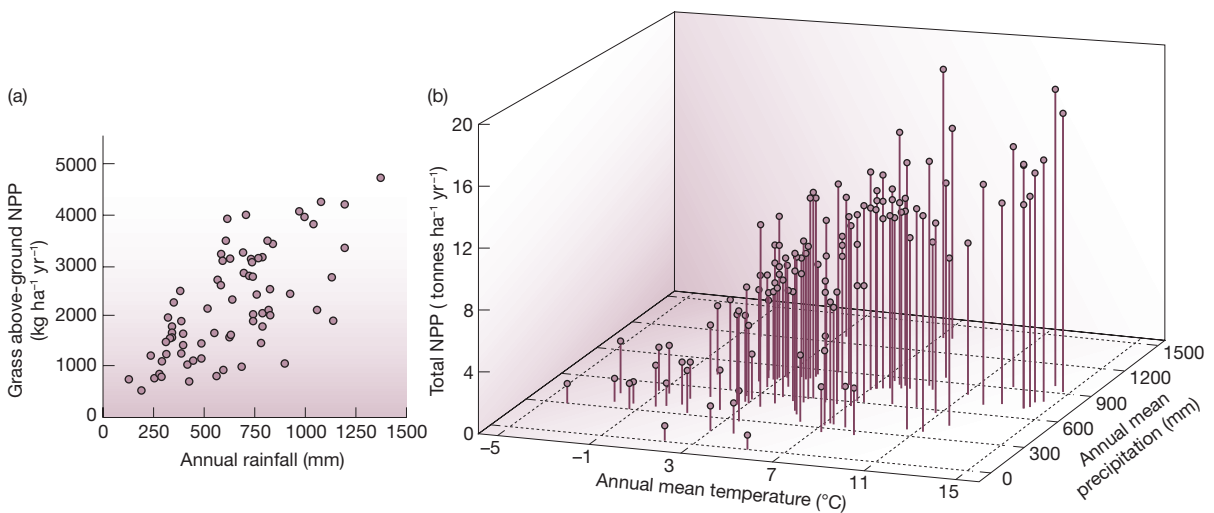
rate of photosynthesis. Carbon dioxide is normally present at a level of around 0.03% of atmospheric gases and seems to play no significant role in determining differences between the productivities of different communities (although global increases in carbon dioxide concentration may bring big changes; Kicklighter et al., 1999). On the other hand, the intensity of radiation, the availability of water and nutrients, and temperature all vary dramatically from place to place. They are all candidates for the role of limiting factor. Which of them actually sets the limit to primary productivity?

Depending on location, something between 0 and 5 J of solar energy strike each square meter of the Earth's surface every minute. If all this were converted by photosynthesis to plant biomass (that is, if photosynthetic efficiency was 100%) there would be a prodigious generation of plant material, ten to a hundred times greater than recorded values. However, only about 44% of incident shortwave radiation occurs at wavelengths suitable for photosynthesis. Yet, even when this is taken into account, productivity still falls well below the maximum possible. For example, the conifer communities shown in Figure 11.1 had the highest net photosynthetic efficiencies, but these were only between 1% and 3%. For a similar level of incoming radiation, deciduous forests achieved 0.5–1%, and, despite their greater energy income, deserts managed only 0.01–0.2%. These can be compared with short-term peak efficiencies achieved by crop plants under ideal conditions, when values from 3% to 10% can be achieved.

There is no doubt that available radiation would be used more efficiently if other resources were in abundant supply. The much higher values of community productivity from agricultural systems bear witness to this. Shortage of water – an essential resource both as a constituent of cells and for photosynthesis – is often the critical factor. It is not surprising, therefore, that the rainfall of a region is quite closely correlated with its productivity (Figure 11.2a). There is also a clear relationship between NPP and mean annual temperature, but note that high temperature is associated with rapid transpiration, and thus higher temperatures increase the rate at which water shortage becomes important. Water shortage has direct effects on the rate of plant growth, but it also leads to less dense vegetation.

terrestrial communities use radiation inefficiently

water and temperature as critical factors



(a) AFTER HIGGINS ET AL., 2000; (b) AFTER LUO ET AL., 2002

**Figure 11.2**

(a) Above-ground net primary productivity (NPP) of grass in savanna regions of the world in relation to annual rainfall. (b) Total NPP in relation to both annual precipitation and temperature on the Tibetan Plateau for ecosystems including forests, woodlands, shrublands, grasslands and desert.

Vegetation that is sparse intercepts less radiation (much of which falls on bare ground), accounting for much of the difference in productivity between desert vegetation and forest in Figure 11.1. Figure 11.2b plots the NPP for a variety of ecosystem types against both temperature and annual rainfall – highest productivity occurs where temperature and rainfall are both high.

The productivity of a community can be sustained only for that part of the year when the plants bear photosynthetically active foliage. Deciduous trees have a self-imposed limit on the period of the year during which they bear foliage, while evergreen trees hold a canopy throughout the year. However, for much of the year conifer forest may barely photosynthesize at all, a pattern that is particularly marked in the colder boreal zones (Figure 11.3).

No matter how brightly the sun shines, how often the rain falls and how equable the temperature, productivity must be low if there is no soil in a terrestrial community, or if the soil is deficient in essential mineral nutrients. Of all the mineral nutrients, the one with the strongest influence on community productivity is fixed nitrogen (in contrast to atmospheric nitrogen, which is not directly available for use in photosynthesis; fixed nitrogen occurs in inorganic ions such as nitrate). There is probably no agricultural or forestry system that does not respond to the application of nitrogen by increasing primary productivity, and this may well be true of natural vegetation as well. The deficiency of other elements, particularly phosphorus, can also hold the productivity of a community far below what is theoretically possible.

In fact, in the course of a year, the productivity of a terrestrial community may be limited by a succession of factors. The primary productivity of grasslands may be far below the theoretical maximum because the winters are too cold and the intensity of radiation is low, the summers are too dry, the rate of nitrogen supply is too slow, or because heavy grazing reduces the standing crop of photosynthetic leaves and much of the incident radiation falls on bare ground.

NPP increases with the length of the growing season

NPP may be low because appropriate mineral resources are deficient

a succession of factors may limit primary productivity through the year

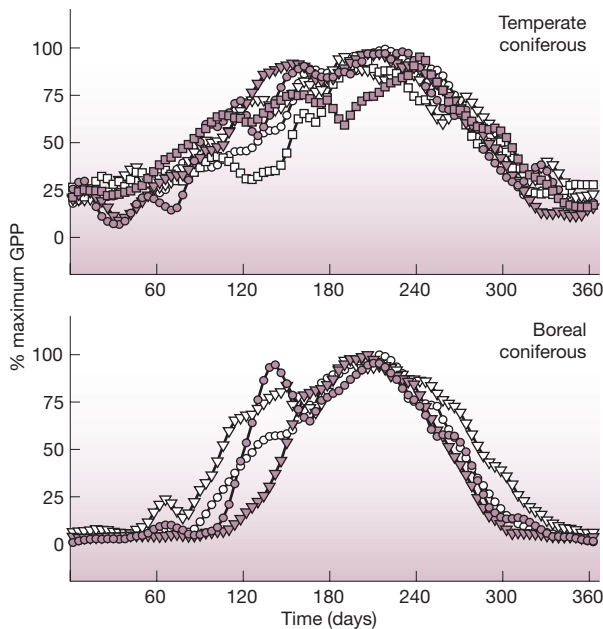


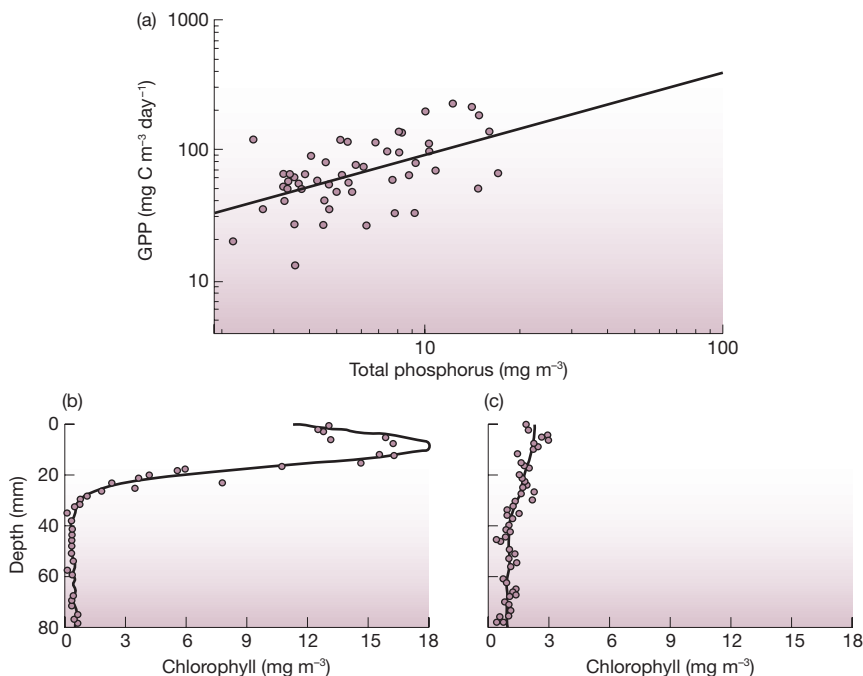
Figure 11.3

Seasonal development of maximum daily gross primary productivity (GPP) for conifer forests in temperate (Europe and North America) and boreal locations (Canada, Scandinavia and Iceland). The different symbols in each panel relate to different forests. Daily GPP is expressed as the percentage of the maximum achieved in each forest during the 365 days of the year. Note the extended periods with no photosynthesis in the colder boreal locations.

AFTER FALGE ET AL., 2002

In aquatic communities, the factors that most frequently limit primary productivity are the availability of nutrients (particularly nitrate and phosphate) and the intensity of solar radiation that penetrates the column of water. Productive aquatic communities occur where, for one reason or another, nutrient concentrations are high (as for the lakes in Figure 11.4a). Lakes receive nutrients by the

productive aquatic communities occur where nutrient concentrations are high



(a) AFTER CARIGNANI ET AL., 2000; (b, c) AFTER SILUWANE ET AL., 2001

Figure 11.4

(a) The relationship between gross primary productivity (GPP) of phytoplankton (microscopic plants) and phosphorus concentration in some Canadian lakes. (b, c) Examples of vertical chlorophyll profiles recorded in the ocean off the coast of Namibia. The biomass of chlorophyll is an index of NPP of ocean phytoplankton. (b) A location associated with ocean upwelling: the nutrient-rich water fuels very high NPP by phytoplankton near the surface, but the dense phytoplankton cells reduce light penetration so that NPP is not detectable in deeper water. (c) A location where nutrient concentrations are much lower: NPP is thus low, but because light can penetrate more deeply, NPP can be detected to a greater depth. All regression lines are statistically significant.

weathering of rocks and soils in their catchment areas, in rainfall and as a result of human activity (fertilizers and sewage input; see Chapter 13); lakes vary considerably in nutrient availability.

In the oceans, locally high levels of primary productivity are associated with high nutrient inputs from two sources. First, nutrients may flow continuously into coastal shelf regions from estuaries. Productivity in the inner shelf region is particularly high because nutrient concentrations are high and the relatively clear water provides a reasonable depth within which net photosynthesis is positive (the *euphotic zone*). Closer to land, the water is richer in nutrients but highly turbid and its productivity is less. The least productive zones are in the open ocean where, although the water is clear and the euphotic zone is deep, there are generally extremely low concentrations of nutrients. Local regions of high productivity occur in the open ocean only where there are upwellings from deep, nutrient-rich water (compare Figure 11.4b and c).

## 11.3 The fate of primary productivity

Fungi, animals and most bacteria are heterotrophs: they derive their matter and energy either directly by consuming plant material or indirectly from plants by eating other heterotrophs. Plants, the primary producers, comprise the first trophic level in a community; primary consumers occur at the second trophic level; secondary consumers (carnivores) at the third, and so on.

### 11.3.1 The relationship between primary and secondary productivity

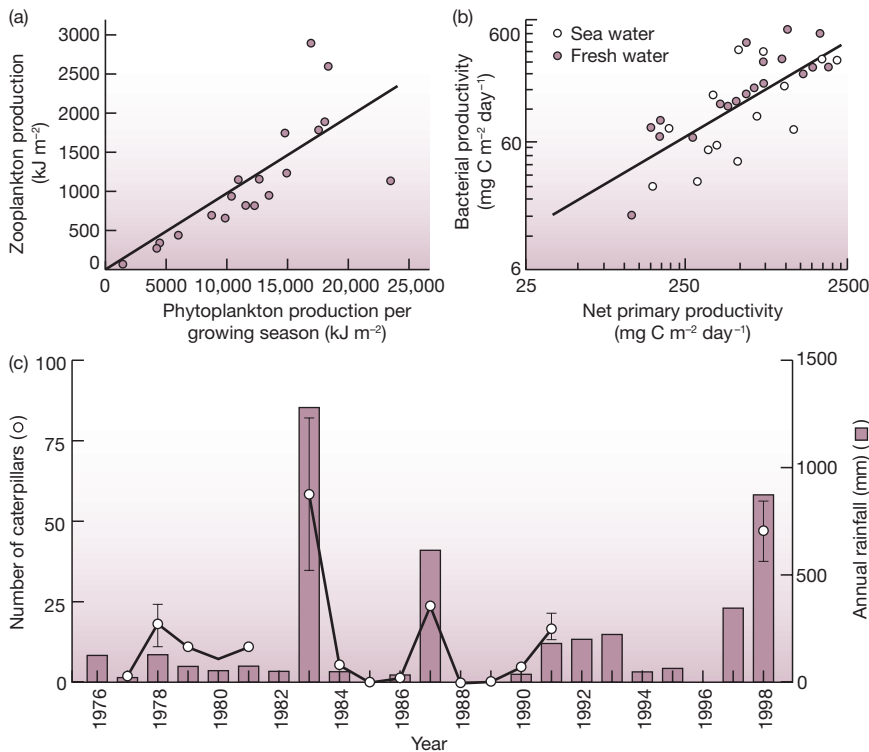
there is a general positive relationship between primary and secondary productivity

Since secondary productivity depends on primary productivity, we should expect a positive relationship between the two variables in communities. Figure 11.5 illustrates this general relationship in aquatic and terrestrial examples. Secondary productivity by zooplankton (small animals in the open water), whose main food is phytoplankton cells, is positively related to phytoplankton productivity in a range of lakes in different parts of the world (Figure 11.5a). The productivity of heterotrophic bacteria in lakes and oceans also parallels that of phytoplankton (Figure 11.5b); the bacteria metabolize dissolved organic matter released from intact phytoplankton cells or produced as a result of ‘messy feeding’ by grazing animals. Figure 11.5c shows how the abundance achieved by caterpillars (larvae of moths and butterflies) is tightly linked to annual rainfall (and thus primary productivity) on an island in the Galapagos Archipelago. One of Darwin’s famous finches, the seed-eating *Geospiza fortis* (see Figure 2.14), also responds to increased plant production in wet years by raising significantly more broods of young (Grant et al., 2000).

most of the primary productivity does not pass through the grazer system

In both aquatic and terrestrial communities, secondary productivity by herbivores is approximately one-tenth of the primary productivity upon which it is based. Where has the missing energy gone? First, not all of the plant biomass produced is consumed alive by herbivores. Much dies without being grazed and supports a community of decomposers (bacteria, fungi and detritivorous animals). Second, not all the plant biomass eaten by herbivores (nor herbivore biomass eaten by

(a) AFTER BRYLINSKY &amp; MANN, 1973; (b) AFTER COLE ET AL., 1988; (c) AFTER GRANT ET AL., 2000


**Figure 11.5**

The relationship between primary and secondary productivity for: (a) zooplankton in lakes, (b) bacteria in fresh and sea water, and (c) caterpillars (numbers and standard errors from a standard census) in relation to a histogram of annual rainfall on the Galapagos island of Daphne Major. Caterpillar numbers are an index of their annual secondary productivity; the primary productivity of plants, upon which the caterpillars feed, is closely correlated with annual rainfall. Regression lines are significant and caterpillar abundance is significantly correlated with annual rainfall at  $P < 0.05$ .

carnivores) is assimilated and available for incorporation into consumer biomass. Some is lost in feces, and this also passes to the decomposers. Third, not all the energy that has been assimilated is actually converted to biomass. A proportion is lost as respiratory heat. This occurs both because no energy conversion process is 100% efficient (some is lost as unusable random heat, consistent with the second law of thermodynamics) and also because the organisms do work that requires energy, again released as heat. These three energy pathways occur at all trophic levels and are illustrated in Figure 11.6.

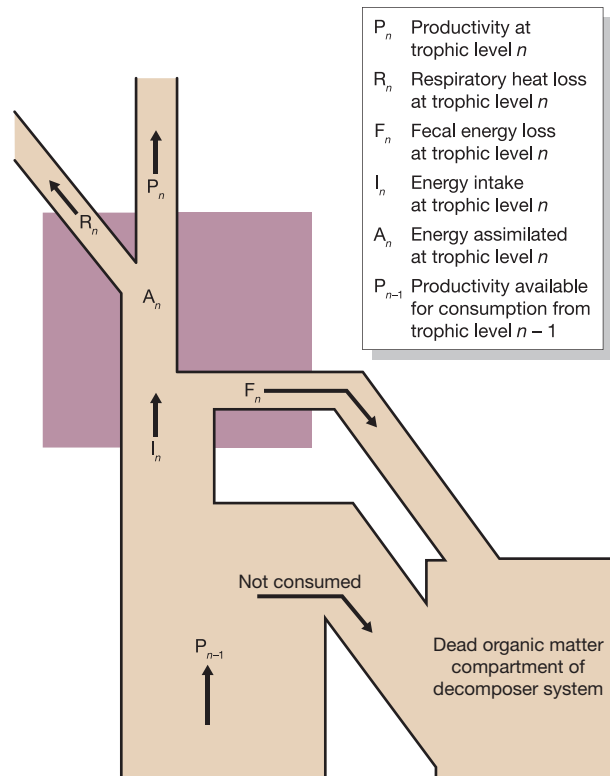
### 11.3.2 The fundamental importance of energy transfer efficiencies

A unit of energy (a joule) may be consumed and assimilated by an invertebrate herbivore that uses part of it to do work and loses it as respiratory heat. Or it might be consumed by a vertebrate herbivore and later be assimilated by a carnivore that dies and enters the dead organic matter compartment. Here, what remains of the joule may be assimilated by a fungus and consumed by a soil mite, which uses it to do work, dissipating a further part of the joule as heat. At each consumption step, what remains of the joule may fail to be assimilated and pass in the feces to dead organic matter, or it may be assimilated and respired, or assimilated and incorporated into growth of body tissue (or the production of offspring). The body may die and what remains of the joule enters the dead organic matter compartment, or it may be captured alive by a consumer in the next trophic level where it meets a further set of possible branching pathways. Ultimately, each

possible pathways of a joule of energy through a community

**Figure 11.6**

The pattern of energy flow through a trophic compartment (represented as the maroon box).



joule will have found its way out of the community, dissipated as respiratory heat at one or more of the transitions in its path along the food chain. Whereas a molecule or ion may cycle endlessly through the food chains of a community, energy passes through just once.

The possible pathways in the herbivore/carnivore (live consumer) and decomposer systems are the same, with one critical exception – feces and dead bodies are lost to the former (and enter the decomposer system), but feces and dead bodies from the decomposer system are simply sent back to the dead organic matter compartment at its base. Thus, the energy available as dead organic matter may finally be completely metabolized – and all the energy lost as respiratory heat – even if this requires several circuits through the decomposer system. The exceptions to this are situations: (i) where matter is exported out of the local environment to be metabolized elsewhere, for example detritus being washed out of a stream; and (ii) where local abiotic conditions have inhibited decomposition and left pockets of incompletely metabolized high-energy matter, otherwise known as oil, coal and peat.

The proportions of net primary production flowing along each of the possible energy pathways depend on *transfer efficiencies* from one step to the next. We need to know about just three categories of transfer efficiency to be able to predict the pattern of energy flow. These are consumption efficiency (CE), assimilation efficiency (AE) and production efficiency (PE).

*Consumption efficiency* is the percentage of total productivity available at one trophic level that is consumed ('ingested') by the trophic level above. For

consumption, assimilation and production efficiencies determine the relative importance of energy pathways

primary consumers, CE is the percentage of joules produced per unit time as NPP that finds its way into the guts of herbivores. In the case of secondary consumers, it is the percentage of herbivore productivity eaten by carnivores. The remainder dies without being eaten and enters the decomposer system. Reasonable average figures for CE by herbivores are approximately 5% in forests, 25% in grasslands and 50% in phytoplankton-dominated communities. As far as carnivores are concerned, vertebrate predators may consume 50–100% of production from vertebrate prey but perhaps only 5% from invertebrate prey, while invertebrate predators consume perhaps 25% of available invertebrate prey production.

*Assimilation efficiency* is the percentage of food energy taken into the guts of consumers in a trophic level that is assimilated across the gut wall and becomes available for incorporation into growth or to do work. The remainder is lost as feces and enters the decomposer system. An ‘assimilation efficiency’ is much less easily ascribed to microorganisms, where food does not pass through a ‘gut’ and feces are not produced. Bacteria and fungi digest dead organic matter externally and, between them, typically absorb almost all the product: they are often said to have AEs of 100%. AEs are typically low for herbivores, detritivores and microbivores (20–50%) and high for carnivores (around 80%). The way that plants allocate production to roots, wood, leaves, seeds and fruits also influences their usefulness to herbivores. Seeds and fruits may be assimilated with efficiencies as high as 60–70%, and leaves with about 50% efficiency, while the AE for wood may be as low as 15%.

*Production efficiency* is the percentage of assimilated energy that is incorporated into new biomass – the remainder is entirely lost to the community as respiratory heat. PE varies according to the taxonomic class of the organisms concerned. Invertebrates in general have high efficiencies (30–40%), losing relatively little energy in respiratory heat. Amongst the vertebrates, ectotherms (whose body temperature varies according to environmental temperature; see Section 3.2.6) have intermediate values for PE (around 10%), whilst endotherms, which expend considerable energy to maintain a constant temperature, convert only 1–2% of assimilated energy into production. Microorganisms, including protozoa, tend to have very high PEs.

The overall *trophic transfer efficiency* from one trophic level to the next is simply  $CE \times AE \times PE$ . In the period after Lindeman’s (1942) pioneering work (see Box 11.1), it was generally assumed that trophic transfer efficiencies were around 10%; indeed some ecologists referred to a 10% ‘law’. However, there is certainly no law of nature that results in precisely one-tenth of the energy that enters a trophic level transferring to the next. For example, a compilation of trophic studies from a wide range of freshwater and marine environments revealed that trophic-level transfer efficiencies varied between about 2% and 24% – although the mean *was* 10.13% (standard error 0.49) (Pauly & Christensen, 1995).

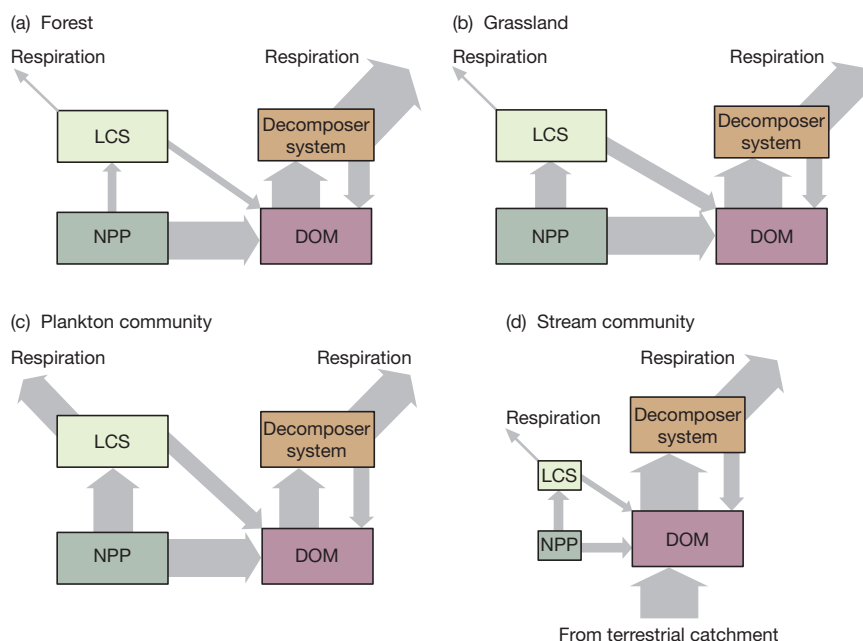
### 11.3.3 The relative roles of the live consumer and decomposer systems

Given knowledge of NPP at a site, and CE, AE and PE for all the trophic groupings present (herbivores, carnivores, decomposers, detritivores), it is possible to map out the relative importance of different pathways. Figure 11.7 does this,

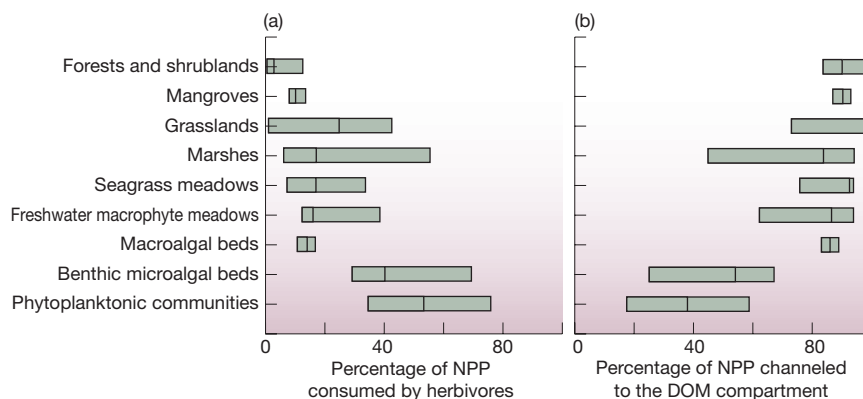


**Figure 11.7**

General patterns of energy flow for: (a) forest, (b) grassland, (c) a plankton community in the sea, and (d) the community of a stream or small pond. Relative sizes of boxes and arrows are proportional to the relative magnitude of compartments and flows. DOM, dead organic matter; LCS, live consumer system; NPP, net primary production.



in a general way, for a forest, a grassland, a plankton community (of the ocean or a large lake) and the community of a small stream or pond. The decomposer system is probably responsible for the majority of secondary production, and therefore respiratory heat loss, in every community in the world (Figure 11.8). The 'live consumers' have their greatest role in open-water aquatic communities based on phytoplankton or in the beds of microalgae that occur in shallow water. In each case, a large proportion of NPP is consumed alive and assimilated at quite

**Figure 11.8**

Box plots for a range of ecosystem types showing: (a) percentage of net primary production (NPP) consumed by herbivores and (b) percentage of NPP entering the dead organic matter (DOM) compartment. Boxes encompass 25% and 75% percentiles of published values and the central lines represent the median values. Phytoplankton and aquatic microalgal communities channel the largest proportions of NPP through herbivores and the smallest proportions through the DOM compartment.

a high efficiency (Figure 11.8a). In contrast, the decomposer system plays its greatest role where vegetation is woody – forests, shrublands and mangroves (Figure 11.8b). Grasslands and aquatic systems based on large plants [seagrasses, freshwater weeds and macroalgae (seaweeds)] occupy intermediate positions.

The live consumer system holds little sway in terrestrial communities because of low herbivore consumption efficiencies and assimilation efficiencies, and it is almost non-existent in many small streams and ponds simply because primary productivity is so low (Figure 11.7d). The latter often depend for their energy base on dead organic matter that falls or is washed or blown into the water from the surrounding terrestrial environment. The deep-ocean benthic community has a trophic structure very similar to that of streams and ponds. In this case, the community lives in water too deep for photosynthesis and energy is derived from dead phytoplankton, bacteria, animals and feces that sink from the autotrophic community in the euphotic zone above. From a different perspective, the ocean bed is equivalent to a forest floor beneath an impenetrable forest canopy.

## 11.4 The process of decomposition

Given the profound importance of the decomposer system, and thus of decomposers (bacteria and fungi) and detritivores, it is important to appreciate the range of organisms and processes involved in decomposition.

*Immobilization* is what occurs when an inorganic nutrient element is incorporated into organic form, primarily during the growth of green plants: for example, when carbon dioxide becomes incorporated into a plant's carbohydrates. Energy (coming, in the case of plants, from the sun) is required for this. Conversely, decomposition involves the release of energy and the *mineralization* of chemical nutrients – the conversion of elements from organic back to an inorganic form. Decomposition is defined as the gradual disintegration of dead organic matter (i.e. dead bodies, shed parts of bodies, feces) and is brought about by both physical and biological agencies. It culminates with complex, energy-rich molecules being broken down by their consumers (decomposers and detritivores) into carbon dioxide, water and inorganic nutrients. Ultimately, the incorporation of solar energy in photosynthesis, and the immobilization of inorganic nutrients into biomass, is balanced by the loss of heat energy and organic nutrients when the organic matter is mineralized.

decomposition defined

### 11.4.1 Decomposers: bacteria and fungi

If a scavenging animal, a vulture or a burying beetle perhaps, does not take a dead resource immediately, the process of decomposition usually starts with colonization by bacteria and fungi. Bacteria and fungal spores are always present in the air and the water, and are usually present on (and often in) dead material before it is dead. The early colonists tend to use soluble materials, mainly amino acids and sugars that are freely diffusible. The residual resources, though, are not diffusible and are more resistant to attack. Subsequent decomposition therefore proceeds more slowly, and involves microbial specialists that can break down structural carbohydrates (e.g. celluloses, lignins) and complex proteins such as suberin (cork) and insect cuticle.

bacteria and fungi are early colonists of newly dead material

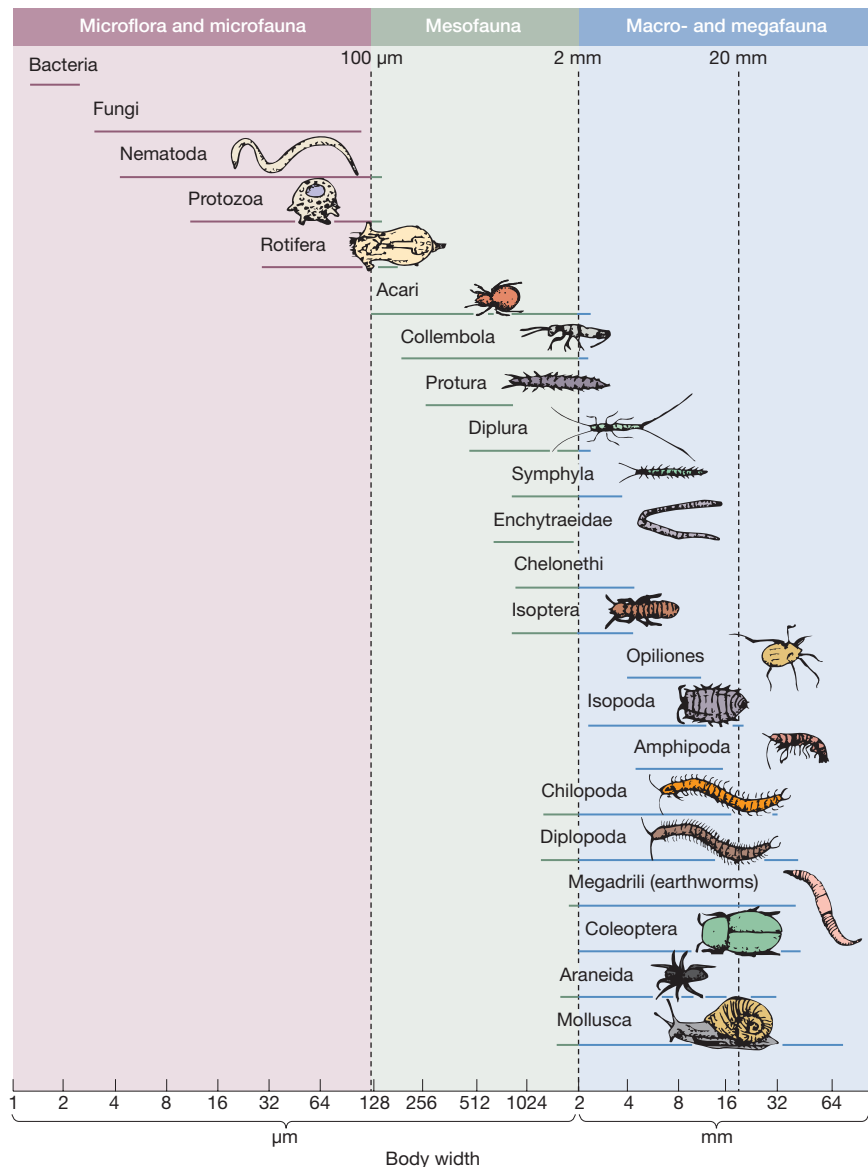
### 11.4.2 Detritivores and specialist microbivores

specialist microbivores feed on bacteria and fungi, but most detritivores consume detritus too

The *microbivores* are a group of animals that operate alongside the detritivores, and which can be difficult to distinguish from them. The name microbivore is reserved for the minute animals that specialize at feeding on bacteria or fungi but are able to exclude detritus from their guts. In fact, though, the majority of detritivorous animals are generalist consumers, of both the detritus itself and the associated bacterial and fungal populations. The invertebrates that take part in the decomposition of dead plant and animal materials are a taxonomically diverse group. In terrestrial environments they are usually classified according to their size (Figure 11.9). This is not an arbitrary basis for classification, because size is

**Figure 11.9**

Size classification by body width of organisms in terrestrial decomposer food webs. Bacteria and fungi are decomposers. Animals that feed on dead organic matter (plus any associated bacteria and fungi) are detritivores. Carnivores that feed on detritivores include Opiliones (harvest spiders), Chilopoda (centipedes) and Araneida (spiders).



an important feature for organisms that reach their resources by burrowing or crawling among cracks and crevices of litter or soil.

In freshwater ecology, on the other hand, the study of detritivores has been concerned less with the size of the organisms than with the ways in which they obtain their food (refer back to Figure 4.16). For example, *shredders* are detritivores that feed on coarse particulate organic matter, such as tree leaves fallen into a river – these animals fragment the material into finer particles. On the other hand, *collector–filterers*, such as larvae of blackflies in rivers, consume the fine particulate organic matter that otherwise would be carried downstream. Because of very high densities (sometimes as many as 600,000 blackfly larvae per square meter of riverbed) a very large quantity of fine particulate matter is converted by the larvae into fecal pellets that settle on the bed and provide food for other detritivores (estimated at an amazing 429 tonnes dry mass of fecal pellets per day in a Swedish river; Malmqvist et al., 2001).

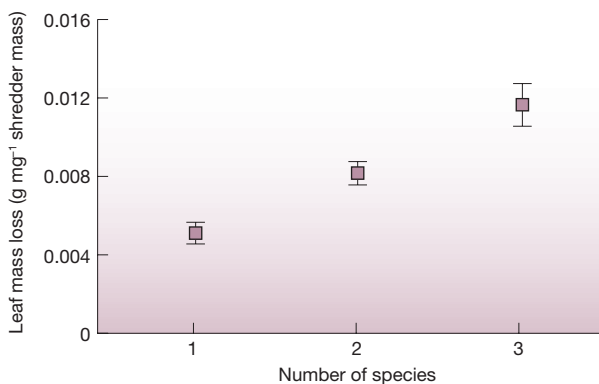
aquatic detritivores are usually classified according to their feeding mode

### 11.4.3 Consumption of plant detritus

Two of the major organic components of dead leaves and wood are cellulose and lignin. These pose considerable digestive problems for animal consumers. Digesting cellulose requires *cellulase* enzymes but, surprisingly, cellulases of animal origin have been definitely identified in only one or two species. The majority of detritivores, lacking their own cellulases, rely on the production of cellulases by associated bacteria or fungi or, in some cases, protozoa. The interactions are of a range of types: (i) *obligate mutualisms* between a detritivore and a specific and permanent gut microflora (e.g. bacteria) or microfauna (e.g. termites); (ii) *facultative mutualisms*, where the animals make use of cellulases produced by a microflora that is ingested with detritus as it passes through an unspecialized gut (e.g. woodlice); or (iii) ‘external rumens’, where animals simply assimilate the products of the cellulase-producing microflora associated with decomposing plant remains or feces [e.g. springtails (*Collembola*)].

A variety of detritivores may be involved in fragmenting a single leaf. In experiments involving larvae of shredding stoneflies in streams, three different species were very similar in the efficiency with which they decomposed leaves of the alder tree, *Alnus incana*. However, average leaf loss was significantly greater when pairs of species were involved and was faster still when all three species were feeding on the leaf (Figure 11.10). The same number of stonefly larvae were

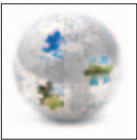
the presence of more species of detritivore increases decomposition rate



**Figure 11.10**

Variation in rate of loss of alder leaf mass in replicated stream experiments (per gram of leaf per milligram of shredder  $\pm$  SE) caused by three species of shredder: larvae of the stoneflies *Protonemura meyeri*, *Nemoura avicularis* and *Taeniopteryx nebulosa*. The results are averaged for species acting on their own, for pairs of species in all possible combinations, and for all three species together (means  $\pm$  SE). The decomposition rate was significantly faster when species operated in pairs, and was fastest of all when all three species were together.

included in every experiment (12 of a single species, six each in the species pairs, and four each when all three species were present) and the results were expressed in a standard way (leaf mass loss per gram of leaf per milligram of shredder in a 46-day experiment) so the result directly reflects the species richness present. These results are indicative of *complementarity* (each species feeds in a slightly different way so their combined effect is enhanced). Studies such as these have significant implications for the role that biological diversity plays in ecosystem functioning. Given current concerns about the extinction of species worldwide (see Chapter 14), we need to know whether diversity loss will have major consequences for the way ecosystems work. This is an important and controversial area (Box 11.2).



## 11.2 Topical ECOncerns

### 11.2 TOPICAL ECOncerns

#### The importance of biological diversity in ecosystem functioning

Ecologists agree that some experimental evidence points to a significant role for biological diversity (biodiversity) in ecosystem functioning. Figure 11.10, for example, showed how decomposition rate is slower when fewer species are involved in the process. But some disagree about how much this matters – in other words, whether these kinds of result prove that biodiversity is critical to ecosystem health. This is a significant question at a time when global biodiversity is declining.

The following quotation comes from a commentary by Jocelyn Kaiser that appeared in 2000 in one of the major academic scientific journals, *Science* (289, 1282–1283).

#### Rift over biodiversity divides ecologists

A long-simmering debate among ecologists over the importance of biodiversity to the health of ecosystems has erupted into a full-blown war. Opposing camps are dueling over the quality of key experiments, and some are flinging barbs at meetings and in journals.

What lay behind such bellicose language? The disagreement began as part of the normal debate that should occur about any piece of research. To

what extent are the conclusions justified from the results and how far can they be generalized from the special circumstances of the experiment to other situations in nature? Various studies around the world seemed to show that the loss of plant or animal species might adversely affect ecosystem function; for example, the productivity of grassland communities appears to be higher when more species are present. This could mean that biodiversity *per se* matters to productivity. But might variables other than species diversity have given rise to increased productivity? For example, perhaps such a result was a statistical artefact – higher productivity with higher species diversity might be explained simply by the addition of a more productive species to the list (and a more productive species is more likely to be present when more species are included in the experiment).

This kind of debate is healthy, but it took on a new dimension when one of the world's leading learned societies, the Ecological Society of America (ESA), published a pamphlet and sent copies to members of Congress. One of a series called 'Issues in Ecology', the pamphlet concerned the importance of biodiversity for ecosystem functioning. It summarized the results of several studies but with little discussion of doubts raised by skeptics in the ESA.

The commentator noted:

Other ecologists safely outside the fray say there is more at stake in this dispute than personalities and egos. Beyond the legitimate scientific question about how much can be learned from experiments is the nagging question – by no means limited to biodiversity – of when scientific data are strong enough to form the basis of policy decisions.

*This debate was not really about the quality of the science (since every study has its limitations), but*

*rather the document that the ESA sent to Congress, which some said tended to present opinion as fact. Do you think scientists should remain entirely outside the political arena? If not, how would you ensure that balanced and generally accepted positions would be presented? Read the article by Hooper et al. (2005) 'Effects of biodiversity on ecosystem functioning: a consensus of current knowledge' in Ecological Monographs 75, 3–35. Decide whether the opposing factions have found an effective way forward – the list of authors includes people who were on different sides of the original debate.*

The decomposition of dead material is not simply due to the sum of the activities of decomposers and detritivores; it is largely the result of interaction between the two (Lussenhop, 1992). This can be illustrated by taking an imaginary journey with a leaf fragment through the process of decomposition, focusing attention on a part of the wall of a single cell. Initially, when the leaf falls to the ground, the piece of cell wall is protected from microbial attack because it lies within the plant tissue. The leaf is now chewed and the fragment enters the gut of a woodlouse. Here it meets a new microbial flora in the gut and is acted on by the digestive enzymes of the woodlouse. The fragment emerges, changed by passage through the gut. It is now part of the woodlouse's feces and is much more easily attacked by microorganisms, because it has been fragmented and partially digested. While microorganisms are colonizing the fecal pellet, it may again be eaten, perhaps by a springtail, and pass through the new environment of the springtail's gut. Incompletely digested fragments may again appear, this time in springtail feces, yet more easily accessible to microorganisms. The fragment may pass through several other guts in its progress from being a piece of dead tissue to its inevitable fate of becoming carbon dioxide and minerals.

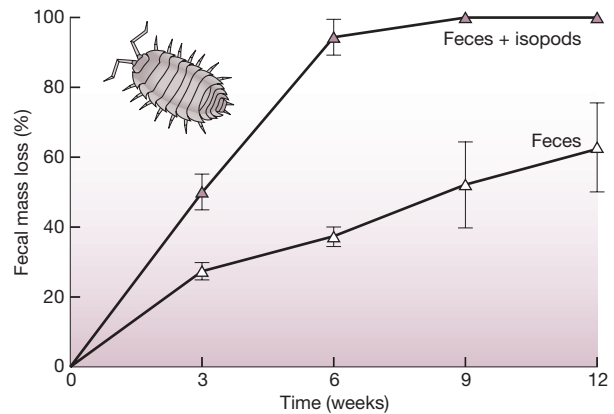
#### 11.4.4 Consumption of feces and carrion

The dung of carnivorous vertebrates is relatively poor-quality stuff. Carnivores assimilate their food with high efficiency (usually 80% or more is digested) and their feces retain only the least digestible components; their decomposition is probably caused almost entirely by bacteria and fungi. In contrast, herbivore dung still contains an abundance of organic matter and is sufficiently thickly spread in the environment to support its own characteristic fauna, consisting of many occasional visitors but with several specific dung-feeders. A good example is provided by elephant dung; within a few minutes of dung deposition the area is alive with beetles. The adult dung beetles feed on the dung but they also bury large quantities along with their eggs to provide food for developing larvae.

All animals defecate and die, yet feces and dead bodies are not generally very obvious in the environment. This is because of the efficiency of the specialist

**Figure 11.11**

The influence of woodlice on the rate of breakdown of feces of herbivorous caterpillars (*Operophtera fagata* – which feed on leaves of beech trees, *Fagus sylvatica*). After 6 weeks, twice as much of the fecal material had decomposed when woodlice were present.



AFTER ZIMMER &amp; TOPP, 2002

consumers of these dead organic products. On the other hand, where consumers of feces are absent, a build-up of fecal material may occur. Figure 11.11 shows how feeding by woodlice (*Porcellio scaber* and *Oniscus asellus*) speeds the breakdown of invertebrate feces. A more dramatic example is provided by the accumulation of cattle dung where these domestic animals have been introduced to locations lacking appropriate dung beetles. In Australia, for example, during the past 200 years, the cow population increased from just seven individuals (brought over by the first English colonists in 1788) to 30 million or so, producing 300 million cowpats per day. The lack of native dung beetles led to losses of up to 2.5 million hectares per year under dung. The decision was made in 1963 to establish in Australia beetles of African origin, able to dispose of bovine dung under the conditions where cattle are raised; more than 20 species have been introduced (Doube et al., 1991).

When considering the decomposition of dead bodies, it is helpful to distinguish three categories of organisms that attack carcasses. As before, decomposers (bacteria and fungi) and invertebrate detritivores have roles to play, but, in addition, scavenging vertebrates are often of considerable importance. Many carcasses of a size to make a single meal for one of a few of these scavenging detritivores will be removed completely within a very short time of death, leaving nothing for bacteria, fungi or invertebrates. This role is played, for example, by Arctic foxes and skuas in polar regions; by crows, gluttons and badgers in temperate areas; and by a wide variety of birds and mammals, including kites, jackals and hyenas, in the tropics.

## 11.5 The flux of matter through ecosystems

Chemical elements and compounds are vital for the processes of life. When living organisms expend energy (as they all do, continually), they do so, essentially, in order to extract chemicals from their environment, and hold on to them and use them for a period before they lose them again. Thus, the activities of organisms profoundly influence the patterns of flux of chemical matter.

The great bulk of living matter in any community is water. The rest is made up mainly of carbon compounds and this is the form in which energy is accumulated



and stored. Carbon enters the food web of a community when a simple molecule, carbon dioxide, is taken up in photosynthesis. Once incorporated in NPP, it is available for consumption as part of a sugar, a fat, a protein or, very often, a cellulose molecule. It follows exactly the same route as energy, being successively consumed and either defecated, assimilated or used in metabolism, during which the energy of its molecule is dissipated as heat while the carbon is released again to the atmosphere as carbon dioxide. Here, though, the tight link between energy and carbon ends.

Once energy is transformed into heat, it can no longer be used by living organisms to do work or to fuel the synthesis of biomass. The heat is eventually lost to the atmosphere and can never be recycled: life on Earth is only possible because a fresh supply of solar energy is made available every day. In contrast, the carbon in carbon dioxide can be used again in photosynthesis. Carbon, and all other nutrient elements (nitrogen, phosphorus, etc.), are available to plants as simple organic molecules or ions in the atmosphere (carbon dioxide), or as dissolved ions in water (nitrate, phosphate, potassium, etc.). Each can be incorporated into complex carbon compounds in biomass. Ultimately, however, when the carbon compounds are metabolized to carbon dioxide, the mineral nutrients are released again in simple inorganic form. Another plant may then absorb them, and so an individual atom of a nutrient element may pass repeatedly through one food chain after another.

Unlike the energy of solar radiation, moreover, nutrients are not in unalterable supply. The process of locking some up into living biomass reduces the supply remaining to the rest of the community. If plants, and their consumers, were not eventually decomposed, the supply of nutrients would become exhausted and life on Earth would cease.

We can conceive of pools of chemical elements existing in compartments. Some compartments occur in the *atmosphere* (carbon in carbon dioxide, nitrogen as gaseous nitrogen, etc.), some in the rocks of the *lithosphere* (calcium as a constituent of calcium carbonate, potassium in the rock called feldspar) and others in the waters of soil, streams, lakes or oceans – the *hydrosphere* (nitrogen in dissolved nitrate, phosphorus in phosphate, carbon in carbonic acid, etc.). In all these cases the elements exist in inorganic form. In contrast, living organisms (the biota) and dead and decaying bodies can be viewed as compartments containing elements in organic form [carbon in cellulose or fat, nitrogen in protein, phosphorus in adenosine triphosphate (ATP), etc.]. Studies of the chemical processes occurring within these compartments and, more particularly, of the fluxes of elements between them, comprise the science of biogeochemistry.

Nutrients are gained and lost by communities in a variety of ways (Figure 11.12). A nutrient budget can be constructed if we can identify and measure all the processes on the credit and debit sides of the equation.

energy cannot be cycled and reused – matter can

biogeochemistry and biogeochemical cycles

### 11.5.1 Nutrient budgets in terrestrial ecosystems

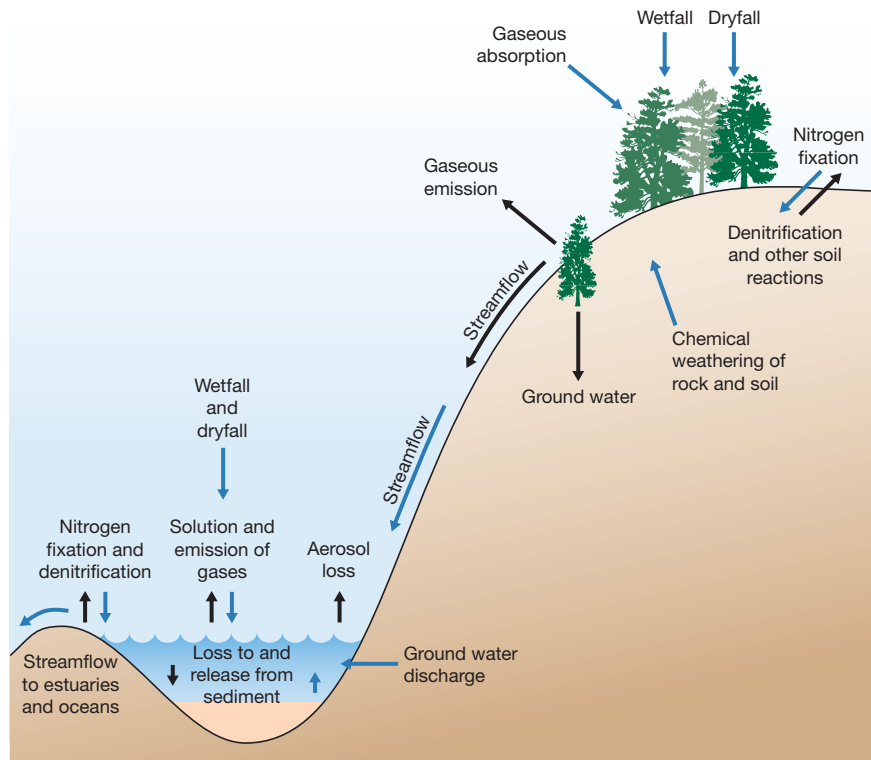
Weathering of parent bedrock and soil, by both physical and chemical processes, is the main source of nutrients such as calcium, iron, magnesium, phosphorus and potassium, which may then be taken up via the roots of plants.

Atmospheric carbon dioxide is the source of the carbon content of terrestrial communities. Similarly, gaseous nitrogen from the atmosphere provides most

nutrient inputs

**Figure 11.12**

Components of the nutrient budgets of a terrestrial and an aquatic system. Inputs are shown in blue and outputs in black. Note how the two communities are linked by streamflow, which is a major output from the terrestrial system but a major input to the aquatic one.



of the nitrogen content of communities. Several types of bacteria and blue-green algae possess the enzyme nitrogenase, which converts gaseous nitrogen to ammonium ions ( $\text{NH}_4^+$ ) that can then be taken up through the roots and used by plants. All terrestrial ecosystems receive some available nitrogen through the activity of free-living, nitrogen-fixing bacteria, but communities containing plants such as legumes and alder trees (*Alnus* spp.), with their root nodules containing symbiotic nitrogen-fixing bacteria (see Section 8.4.6), may receive a very substantial proportion of their nitrogen in this way.

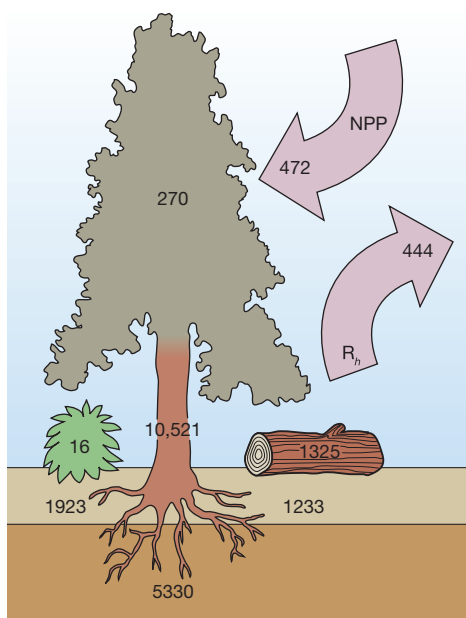
Other nutrients from the atmosphere become available to communities in *dryfall* (settling of particles during periods without rain) or *wetfall* (in rain, snow and fog). Rain is not pure water but contains chemicals derived from a number of sources: (i) trace gases, such as oxides of sulfur and nitrogen; (ii) aerosols, produced when tiny water droplets from the oceans evaporate in the atmosphere and leave behind particles rich in sodium, magnesium, chloride and sulfate; and (iii) dust particles from fires, volcanoes and windstorms, often rich in calcium, potassium and sulfate. Nutrients dissolved in precipitation mostly become available to plants when the water reaches the soil and can be taken up by plant roots.

Nutrients may circulate within the community for many years. Alternatively, the atom may pass through the system in a matter of minutes, perhaps without interacting with the biota at all. Whatever the case, the atom will eventually be lost through one of the variety of processes that remove nutrients from the system (Figure 11.12). These processes constitute the debit side of the nutrient budget equation.

nutrient outputs

Figure 11.13

Annual carbon budget for a ponderosa pine (*Pinus ponderosa*) forest in Oregon, USA, where the trees are up to 250 years old. The numbers above ground represent the amount of carbon contained in tree foliage, in the remainder of forest biomass, in understorey plants and in dead wood on the forest floor. The numbers just below the ground surface represent tree roots (left) and litter (right). The lowest numeral is for soil carbon. The amounts of carbon stored in each of these elements of biomass are in  $\text{g C m}^{-2}$ . Values for net primary production (NPP) and for respiratory heat loss from heterotrophs ( $R_h$ ) (i.e. microorganisms and animals) are in  $\text{g C m}^{-2} \text{ yr}^{-1}$  (arrows). There is an approximate balance in the rate at which carbon is taken up in NPP and the rate at which it is lost as respiratory heat loss.



AFTER LAW ET AL., 2001

Release to the atmosphere is one pathway of nutrient loss. In many communities there is an approximate annual balance in the carbon budget; the carbon fixed by photosynthesizing plants is balanced by the carbon released to the atmosphere as carbon dioxide from the respiration of plants, microorganisms and animals (Figure 11.13). Plants themselves may be direct sources of gaseous and particulate release. For example, forest canopies produce volatile hydrocarbons (e.g. terpenes) and tropical forest trees appear to emit aerosols containing phosphorus, potassium and sulfur. Finally, ammonia gas is released during the decomposition of vertebrate excreta. Other pathways of nutrient loss are important in particular instances. For example, fire (either natural, or when, for instance, agricultural practice includes the burning of stubble) can turn a very large proportion of a community's carbon into carbon dioxide in a very short time, and the loss of nitrogen, as volatile gas, can be equally dramatic.

For many elements, the most substantial pathway of loss is in streamflow. The water that drains from the soil of a terrestrial community into a stream carries a load of nutrients that is partly dissolved and partly particulate. With the exception of iron and phosphorus, which are not mobile in soils, the loss of plant nutrients is predominantly in solution. Particulate matter in streamflow occurs both as dead organic matter (mainly tree leaves) and as inorganic particles.

It is the movement of water under the force of gravity that links the nutrient budgets of terrestrial and aquatic communities (see Figure 11.12). Terrestrial systems lose dissolved and particulate nutrients into streams and ground waters; aquatic systems (including the stream communities themselves, and ultimately the oceans) gain nutrients from streamflow and groundwater discharge. Refer to Section 1.3.3 for discussion of a study (at Hubbard Brook) that explored the chemical linkages at the land–water interface.

### 11.5.2 Nutrient budgets in aquatic communities

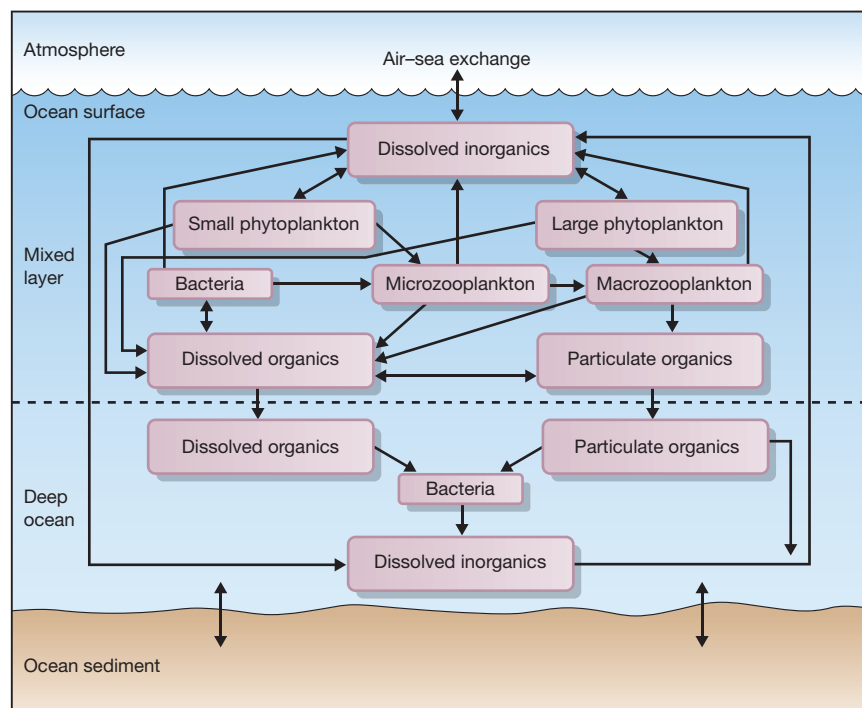
Aquatic systems receive the bulk of their supply of nutrients from stream inflow. In stream and river communities, and also in lakes with a stream outflow, export in outgoing stream water is a major factor. By contrast, in lakes without an outflow (or where this is small relative to lake volume), and also in oceans, nutrient accumulation in permanent sediments is often the major export pathway.

Many lakes in arid regions, lacking a stream outflow, lose water only by evaporation. The waters of these *endorheic* lakes (the word means ‘internal flow’) are thus more concentrated than their freshwater counterparts, being particularly rich in sodium but also in other nutrients such as phosphorus. Saline lakes should not be considered as oddities; globally, they are just as abundant in terms of numbers and volume as freshwater lakes (Williams, 1988). They are usually very fertile with dense populations of blue-green algae, and some, such as Lake Nakuru in Kenya, support huge aggregations of plankton-filtering flamingoes (*Phoeniconaias minor*).

The largest of all endorheic ‘lakes’ is the world ocean – a huge basin of water supplied by the world’s rivers and losing water only by evaporation. Its great size, in comparison to the input from rain and rivers, leads to a remarkably constant chemical composition. The main transformers of dissolved inorganic carbon (essentially carbon dioxide dissolved from the atmosphere) are small phytoplankton cells, whose carbon is mainly recycled near the ocean surface via consumption by microzooplankton, release of dissolved organic substances and their mineralization by bacteria (Figure 11.14). In contrast, pathways involving larger phytoplankton and macrozooplankton are responsible for the majority

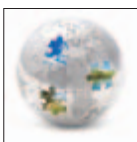
**Figure 11.14**

Pathways of carbon atoms in the ocean. Small phytoplankton, microzooplankton and bacteria recycle carbon in the mixed surface layer. Most of the carbon that moves to the deep ocean follows pathways involving larger phytoplankton and macrozooplankton, to be recycled again. A small proportion of remineralized inorganic carbon and particulate organic carbon is lost to the ocean sediment.



of carbon flux to the deep ocean floor. Some of this organic material is consumed by deep-sea animals, some is mineralized to inorganic form by bacteria and recirculated, and a small proportion becomes buried in the sediment. Figure 11.14 is essentially the ocean equivalent of the forest system in Figure 11.13. In contrast to the atmospheric source of carbon, nutrients such as phosphorus come from two sources – river inputs and water welling up from the deep. Phosphorus atoms in the surface water follow a similar set of pathways to carbon atoms, with about 1% of detrital phosphorus being lost to the deep sediment during each oceanic mixing cycle.

All water bodies receive nutrients, in inorganic and organic form, in the water draining from the land. It is no surprise, therefore, that human activities are responsible for dramatic changes in nutrient fluxes both locally (Box 11.3) and globally. We turn to global biogeochemical cycles in the next section.



## 11.3 Topical ECOncerns

### 11.3 TOPICAL ECONCERNS

#### Nutrient enrichment of aquatic ecosystems: a major problem for lakes and oceans

The excess input of nutrients from sources such as agricultural runoff and sewage has caused many 'healthy' *oligotrophic* lakes (low nutrients, low plant productivity with abundant water weeds, and clear water) to switch to a *eutrophic* condition where high nutrient inputs lead to high phytoplankton productivity (sometimes dominated by toxic bloom-forming species), making the water turbid, shading out large plants and, in the worst situations, leading to anoxia and fish kills. This process of *cultural eutrophication* of lakes has been understood for some time. But it was only recently that people noticed huge 'dead zones' in the oceans near river outlets, particularly those draining large catchment areas such as the Mississippi in North America and the Yangtze in China. The following extracts are from a news item posted by Associated Press on March 29, 2004.

##### Ocean dead zones on the increase

So-called 'dead zones', oxygen-starved areas of the world's oceans that are devoid of fish, top the list of emerging environmental challenges, the United Nations Environment Program [UNEP] warned Monday in its global overview.

The new findings tally nearly 150 dead zones around the globe . . . The main cause is excess nitrogen run-off from farm fertilizers, sewage and industrial pollutants. The nitrogen triggers blooms of microscopic algae known as phytoplankton. As the algae die and rot, they consume oxygen, thereby suffocating everything from clams and lobsters to oysters and fish.

'Human kind is engaged in a gigantic, global, experiment as a result of inefficient and often overuse of fertilizers, the discharge of untreated sewage and the ever rising emissions from vehicles and factories', UNEP Executive Director Klaus Toepfer said in a statement. 'Unless urgent action is taken to tackle the sources of the problem, it is likely to escalate rapidly.'

(All content © MMIV The Associated Press and may not be published, broadcast, rewritten or redistributed. All rights reserved.)

*Suggest some 'urgent actions' that could be taken to alleviate the problem.*

## 11.6 Global biogeochemical cycles

Nutrients are moved over vast distances by winds in the atmosphere and by the moving waters of streams and ocean currents. There are no boundaries, either natural or political. It is appropriate, therefore, to conclude this chapter by moving to an even larger spatial scale to examine global biogeochemical cycles.

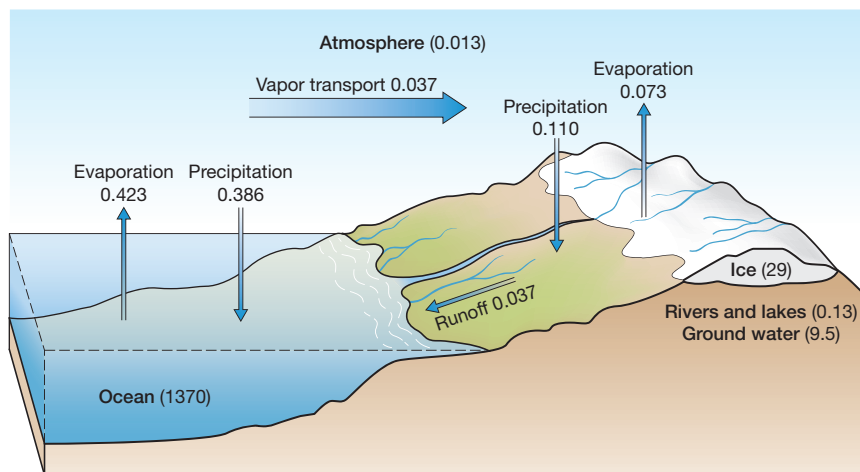
### 11.6.1 The hydrological cycle

The principal source of water is the oceans; radiant energy makes water evaporate into the atmosphere, winds distribute it over the surface of the globe and precipitation brings it down to the Earth's surface (with a net movement of atmospheric water from oceans to continents), where it may be stored temporarily in soils, lakes and icefields (Figure 11.15). Loss occurs from the land through evaporation and transpiration or as liquid flow through stream channels and groundwater aquifers, eventually to return to the sea. The major pools of water occur in the oceans (97.3% of the total for the biosphere), the ice of polar icecaps and glaciers (2.06%), deep in the ground water (0.67%) and in rivers and lakes (0.01%) (Berner & Berner, 1987). The proportion that is in transit at any time is very small – water draining through the soil, flowing along rivers and present as clouds and vapor in the atmosphere – together this constitutes only about 0.08% of the total. However, this small percentage plays a crucial role, both by supplying the requirements for the survival of living organisms and for community productivity and because so many chemical nutrients are transported with the water as it moves.

The hydrological cycle would proceed whether or not a biota was present. However, terrestrial vegetation can modify the fluxes that occur. Vegetation can intercept water at two points on this journey, stopping some from reaching the ground water and moving it back into the atmosphere, by: (i) catching some in foliage from which it evaporates; and (ii) preventing some from draining from the soil water by taking it up via the roots into the plant's transpiration stream. We have seen earlier how cutting down the forest in a catchment in Hubbard Brook (see Section 1.3.3) increased the throughput of water to streams, along with its load of dissolved and particulate matter. It is small wonder that large-scale

**Figure 11.15**

The hydrological cycle, showing volumes of water in the 'reservoirs' of oceans, ice (polar and glacier), rivers and lakes, ground water and atmosphere (units of  $10^6 \text{ km}^3$ ), and on the move as precipitation, runoff, evaporation and vapor transport (arrows: units of  $10^6 \text{ km}^3 \text{ yr}^{-1}$ ).



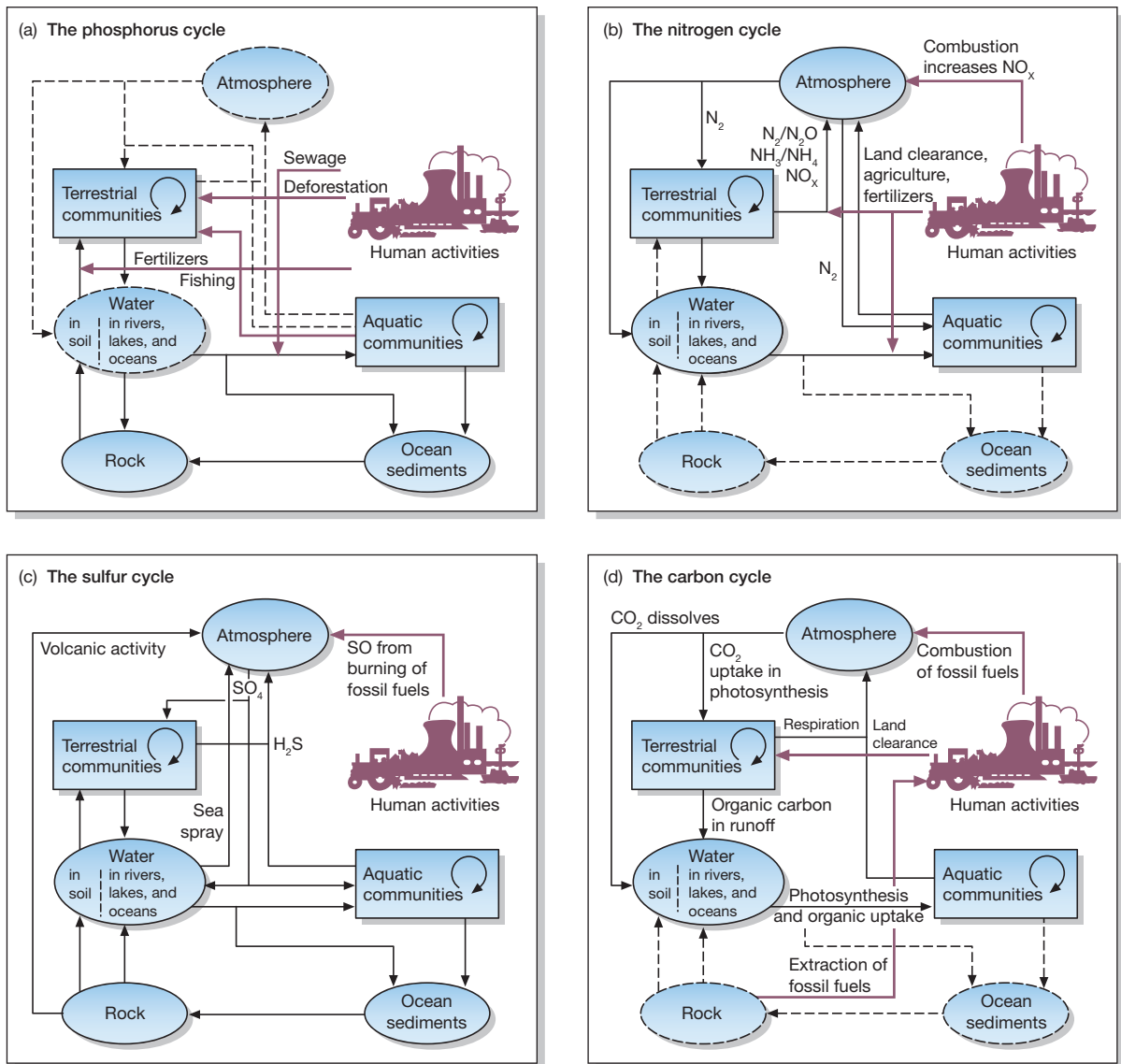


Figure 11.16

The major global pathways of nutrients between the abiotic 'reservoirs' of atmosphere, water (hydrosphere) and rock and sediments (lithosphere), and the biotic 'reservoirs' constituted by terrestrial and aquatic communities. Human activities (maroon arrows) change nutrient fluxes in terrestrial and aquatic communities by releasing extra nutrients into both atmosphere and water. Cycles are presented for four important nutrient elements: (a) phosphorus, (b) nitrogen, (c) sulfur and (d) carbon. Insignificant compartments and fluxes are represented by dashed lines.

deforestation around the globe, usually to create new agricultural land, can lead to loss of topsoil, nutrient impoverishment and increased severity of flooding. Water is a very valuable commodity, and this is reflected in the difficult political exercise of dealing with competing demands – to divert river water for hydro-electric power generation or agricultural irrigation as opposed to maintaining the intrinsic values of an unmanipulated river.

The world's major abiotic reservoirs for nutrients are illustrated in Figure 11.16. We now consider these cycles in turn.



### 11.6.2 The phosphorus cycle

The principal stocks of phosphorus occur in the waters of soil, rivers, lakes and oceans and in rocks and ocean sediments. The phosphorus cycle may be described as a sedimentary cycle because of the general tendency for mineral phosphorus to be carried from the land inexorably to the oceans where ultimately it becomes incorporated in the sediments (Figure 11.16a).

the life history of a phosphorus atom

A 'typical' phosphorus atom, released from the rock by chemical weathering, may enter and cycle within the terrestrial community for years, decades or centuries before it is carried via the ground water into a stream. Within a short time of entering the stream (weeks, months or years), the atom is carried to the ocean. It then makes, on average, about 100 round trips between surface and deep waters, each lasting perhaps 1000 years. During each trip, it is taken up by surface-dwelling organisms, before eventually settling into the deep again. On average, on its 100th descent (after 10 million years in the ocean) it fails to be released as soluble phosphorus, but instead enters the bottom sediment in particulate form. Perhaps 100 million years later, the ocean floor is lifted up by geological activity to become dry land. Thus, our phosphorus atom will eventually find its way back via a river to the sea, and to its existence of cycle (biotic uptake and decomposition) within cycle (ocean mixing) within cycle (continental uplift and erosion).

### 11.6.3 The nitrogen cycle

the nitrogen cycle has an atmospheric phase of overwhelming importance

The atmospheric phase predominates in the global nitrogen cycle, in which nitrogen fixation and denitrification by microbial organisms are of particular importance (Figure 11.16b). However, nitrogen from certain geological sources may also be locally significant in fueling productivity in terrestrial and freshwater communities (Holloway et al., 1998, Thompson et al., 2001). The magnitude of the flux in streamflow from terrestrial to aquatic communities is relatively small, but it is by no means insignificant for the aquatic systems involved. This is because nitrogen is one of the two elements (along with phosphorus) that most often limit plant growth. Finally, there is a small annual loss of nitrogen to ocean sediments.

### 11.6.4 The sulfur cycle

Three natural biogeochemical processes release sulfur to the atmosphere: the formation of seaspray aerosols, anaerobic respiration by sulfate-reducing bacteria and volcanic activity (relatively minor) (Figure 11.16c). Sulfur bacteria release reduced sulfur compounds, particularly  $\text{H}_2\text{S}$ , from waterlogged bog and marsh communities and from tidal mudflats. A reverse flow from the atmosphere involves oxidation of sulfur compounds to sulfate, which returns to earth as both wetfall and dryfall.

the sulfur cycle has an atmospheric phase and a lithospheric phase of similar magnitude

The weathering of rocks provides about half the sulfur draining off the land into rivers and lakes, the remainder coming from atmospheric sources. On its way to the ocean, a proportion of the available sulfur (mainly dissolved sulfate) is taken up by plants, passed along food chains and, via decomposition processes, becomes available again to plants. However, in comparison to phosphorus and nitrogen, a much smaller fraction of sulfur takes part in internal recycling in terrestrial and aquatic communities. Finally, there is a continuous loss of sulfur to ocean sediments.

### 11.6.5 The carbon cycle

Photosynthesis and respiration are the two opposing processes that drive the global carbon cycle. It is predominantly a gaseous cycle, with carbon dioxide as the main vehicle of flux between atmosphere, hydrosphere and biota. Historically, the lithosphere played only a minor role; fossil fuels lay as dormant reservoirs of carbon until human intervention in recent centuries (Figure 11.16d).

Terrestrial plants use atmospheric carbon dioxide as their carbon source for photosynthesis, whereas aquatic plants use dissolved carbonates (i.e. carbon from the hydrosphere). The two subcycles are linked by exchanges of carbon dioxide between atmosphere and oceans. In addition, carbon finds its way into inland waters and oceans as bicarbonate resulting from weathering (carbonation) of calcium-rich rocks such as limestone and chalk. Respiration by plants, animals and microorganisms releases the carbon locked in photosynthetic products back to the atmospheric and hydrospheric carbon compartments.

the opposing forces of photosynthesis and respiration drive the global carbon cycle

### 11.6.6 Human impacts on biogeochemical cycles

It goes almost without saying that human activities contribute significant inputs of nutrients to ecosystems and disrupt local and global biogeochemical cycles. For example, the amounts of carbon dioxide and oxides of nitrogen and sulfur in the atmosphere have been increased by the burning of fossil fuels and by car exhausts, and the concentrations of nitrate and phosphate in stream water have been raised by agricultural practices and sewage disposal. These changes have far-reaching consequences, which will be discussed in Chapter 13.



## Summary

#### Patterns in primary productivity

Primary production on land is limited by a variety of factors – the quality and quantity of solar radiation, the availability of water, nitrogen and other key nutrients, and physical conditions, particularly temperature. Productive aquatic communities occur where, for one reason or another, nutrient concentrations are unusually high and the intensity of radiation is not limiting.

#### The fate of primary productivity

Secondary productivity by herbivores is approximately an order of magnitude less than the primary productivity on which it is based. Energy is lost at each feeding step because consumption efficiencies,

assimilation efficiencies and production efficiencies are all less than 100%. The decomposer system processes much more of a community's energy and matter than the live consumer system. The energy pathways in the live consumer and decomposer systems are the same, with one critical exception – feces and dead bodies are lost to the grazer system (and enter the decomposer system), but feces and dead bodies from the decomposer system are simply sent back to the dead organic matter compartment at its base.

#### The process of decomposition

Decomposition results in complex, energy-rich molecules being broken down by their consumers

(decomposers and detritivores) into carbon dioxide, water and inorganic nutrients. Ultimately, the incorporation of solar energy in photosynthesis, and the immobilization of inorganic nutrients into biomass, is balanced by the loss of heat energy and organic nutrients when the organic matter is decomposed. This is brought about partly by physical processes, but mainly by decomposers (bacteria and fungi) and detritivores (animals that feed on dead organic matter).

### The flux of matter through ecosystems

Nutrients are gained and lost by communities in a variety of ways. Weathering of parent bedrock and soil, by both physical and chemical processes, is the dominant source of nutrients such as calcium, iron, magnesium, phosphorus and potassium, which may then be taken up via the roots of plants. Atmospheric carbon dioxide and gaseous nitrogen are the principal sources of the carbon and nitrogen content of terrestrial communities while other nutrients from the atmosphere become available as dryfall or in rain, snow and fog. Nutrients are lost again through release to the atmosphere or in the water that feeds into streams and rivers. Aquatic systems (including the stream communities themselves, and ultimately the

oceans) gain nutrients from streamflow and ground-water discharge and from the atmosphere by diffusion across their surfaces.

### Global biogeochemical cycles

The principal source of water in the hydrological cycle is the oceans; radiant energy makes water evaporate into the atmosphere, winds distribute it over the surface of the globe and precipitation brings it down to the Earth's surface. Phosphorus derives mainly from the weathering of rocks (lithosphere); its cycle may be described as sedimentary because of the general tendency for mineral phosphorus to be carried from the land inexorably to the oceans where ultimately it becomes incorporated in the sediments. The sulfur cycle has an atmospheric phase and a lithospheric phase of similar magnitude. The atmospheric phase is predominant in both the global carbon and nitrogen cycles. Photosynthesis and respiration are the two opposing processes that drive the global carbon cycle, while nitrogen fixation and denitrification by microbial organisms are of particular importance in the nitrogen cycle. Human activities contribute significant inputs of nutrients to ecosystems and disrupt local and global biogeochemical cycles.

## Review questions

### REVIEW QUESTIONS

Asterisks indicate challenge questions

- 1 A large proportion of the open ocean is, in effect, a marine desert. Why?
- 2\* Describe the general latitudinal trends in net primary productivity. Suggest reasons why such a latitudinal trend does not occur in the oceans.
- 3\* Table 11.2 presents the results of a study that contrasted the productivity of a deciduous beech forest (*Fagus sylvatica*) with that of a

nearby evergreen spruce forest (*Picea abies*). The beech leaves photosynthesized at a greater rate (per gram dry weight) than those of spruce, and beech 'invested' a considerably greater amount of biomass in its leaves each year. But net primary productivity of the beech forest was lower than spruce forest. Why? If these species were grown together, which would you expect to come to dominate the forest? What factors other than productivity might influence the relative competitive status of the two species?

Table 11.2

Characteristics of representative trees of two contrasting species growing within 1 km of each other on the Solling Plateau, Germany.

	BEECH	NORWAY SPRUCE
Age (years)	100	89
Height (m)	27	25.6
Leaf shape	Broad	Needle
Annual production of leaves	Higher	Lower
Photosynthetic capacity per unit dry weight of leaf	Higher	Lower
Length of growing season (days)	176	260
Net primary productivity (metric tons of carbon per hectare per year)	8.6	14.9

AFTER SCHULZE, 1970; SCHULZE ET AL., 1977A, 1977B

- 4 What evidence suggests that the productivity of many terrestrial and aquatic communities is limited by nutrients?
- 5\* In both aquatic and terrestrial communities, secondary productivity by herbivores is

approximately one-tenth of the primary productivity upon which it is based. This has led some to suggest the operation of a 10% law. Do you subscribe to this view?

- 6 Account for the observation that in most communities much more energy is processed through the decomposer system than through the live consumer system.
- 7 Outline the role played by bacteria and fungi (decomposers) in the flux of energy and matter through a named ecosystem. Imagine what would happen if bacteria and fungi were magically removed – describe the resulting scenario.
- 8 Energy cannot be cycled and reused but matter can. Discuss this assertion and its significance for ecosystem functioning.
- 9 Is the ocean simply a large lake in terms of patterns of flux of energy and matter?
- 10 The hydrological cycle would proceed whether or not a biota was present. Discuss how the presence of vegetation modifies the flow of water through an ecosystem.





An aerial photograph of a landscape featuring a winding road that cuts through a patchwork of agricultural fields. The fields are in various shades of brown, tan, and light green, suggesting different crops or stages of growth. The road is a dark, straight line that curves through the landscape. The overall scene is captured from a high angle, providing a clear view of the terrain and the road's path.

# PART FOUR

## Applied Issues in Ecology

**12** | Sustainability 389

**13** | Habitat degradation 423

**14** | Conservation 455





# Chapter 12



## Sustainability

### *Chapter contents*

#### CHAPTER CONTENTS

- 12.1 Introduction
- 12.2 The human population ‘problem’
- 12.3 Harvesting living resources from the wild
- 12.4 The farming of monocultures
- 12.5 Pest control
- 12.6 Integrated farming systems
- 12.7 Forecasting agriculturally driven global environmental change

### *Key concepts*

#### KEY CONCEPTS

In this chapter you will:

- appreciate the underlying dynamics of human population growth and its relationship to the sustainable (or unsustainable) use of resources
- understand the biological basis of sustainable harvesting of wild populations – particularly in fisheries
- recognize the benefits and costs of farming monocultures
- understand that much agricultural practice has not been sustainable because of loss and degradation of soil
- appreciate that water may be the least sustainable of global resources
- recognize the benefits and costs of different methods of pest control and the importance of devising integrated management practices

*The sustainability of human activities, and of the size and distribution of the human population, have increasingly become preoccupations of the general public and of the politicians who represent them. But attaining or even approaching sustainability requires more than a will to do so – it requires ecological understanding, carefully acquired and even more carefully applied.*

## 12.1 Introduction

what is 'sustainability'?

To call an activity 'sustainable' means that it can be continued or repeated for the foreseeable future. Concern has arisen, therefore, precisely because so much human activity is clearly unsustainable. We cannot go on increasing the size of the global human population; we cannot (if we wish to have fish to eat in future) continue to remove fish from the sea faster than the remaining fish can replace their lost companions; we cannot continue to harvest agricultural crops or forests if the quality and quantity of the soil deteriorates or water resources become inadequate; we cannot continue to use the same pesticides if increasing numbers of pests become resistant to them; we cannot maintain the diversity of nature if we continue to drive species to extinction.

Sustainability has thus become one of the core concepts – perhaps *the* core concept – in an ever-broadening concern for the fate of the Earth and the ecological communities that occupy it. In defining sustainability we used the words '*foreseeable* future'. We did so because, when an activity is described as sustainable, it is on the basis of what is known at the time. But many factors remain unknown or unpredictable. Things may take a turn for the worse (as when adverse oceanographic conditions damage a fishery already threatened by overexploitation), or some unforeseen additional problem may be discovered (resistance may appear to some previously irresistible pesticide). On the other hand, technological advances may allow an activity to be sustained that previously seemed unsustainable (new types of pesticide may be discovered that are more finely targeted on the pest itself rather than species that are innocent bystanders). However, there is a real danger that we observe the many technological and scientific advances that have been made in the past and act on the faith that there will always be a technological 'fix' coming along to solve our present problems, too. Unsustainable practices cannot be accepted simply from faith that future advances will make them sustainable after all.

sustainability 'comes of age'

The recognition of sustainability's importance as a unifying idea in applied ecology has grown gradually, but there is something to be said for the claim that sustainability really came of age in 1991. This was when the Ecological Society of America published 'The sustainable biosphere initiative: an ecological research agenda', 'a call-to-arms for all ecologists' with a list of 16 co-authors (Lubchenco et al., 1991). And in the same year, the World Conservation Union, the United Nations Environment Program and the World Wide Fund for Nature jointly published *Caring for the Earth. A Strategy for Sustainable Living*

(IUCN/UNEP/WWF, 1991). The detailed contents of these documents are less important than their existence. They indicate a growing preoccupation with sustainability, shared by scientists and pressure groups, and recognition that much of what we do is not sustainable.

The emphasis shifted more recently from a purely ecological perspective to one that incorporates economic and social conditions that influence sustainability (Milner-Gulland & Mace, 1998), a theme that has gathered pace in the new millennium. Thus, the Millennium Ecosystem Assessment, based on contributions from a large number of natural and social scientists, has as its aim providing both the general public and decision-makers with ‘a scientific evaluation of the consequences of current and projected changes in ecosystems for human well-being’ (Balmford & Bond, 2005; Millennium Ecosystem Assessment, 2005).

In this chapter, we first consider the size and rate of growth of the human population, a primary driver of the environmental problems that confront us (Section 12.2). Then we deal with two areas of applied ecology where sustainability is a particularly pressing issue – the harvesting of living resources from the wild (Section 12.3) and the production, in unnatural agroecosystems, of the food and fiber needs of humankind (Sections 12.4–12.7).

## 12.2 The human population ‘problem’

### 12.2.1 Introduction

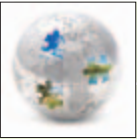
The root of most, if not all of the environmental problems facing us is the ‘population problem’, the effects of a large and growing population of humans. More people means an increased requirement for energy, a greater drain on non-renewable resources like oil and minerals, more pressure on renewable resources like fish and forests (Section 12.3), more need for food production through agriculture (Section 12.4) and so on. The issue is undoubtedly one of sustainability: things cannot go on the way they are. Yet it is not clear exactly what ‘the problem’ is (Box 12.1). Here, therefore, we examine first the size and growth rate of the global human population and how we reached our current state, then how successful we can expect to be in projecting forward into the future, before finally addressing ‘the problem’ more directly by asking the question, ‘How many people can the Earth support?’

what is the human population problem?

### 12.2.2 Population growth up to the present

When the finger is pointed at human population *growth* as the key issue, it is often said that what is wrong is that the global population has been growing ‘exponentially’. But in an exponentially growing population (see Chapter 5) the rate of increase per individual is constant. The population as a whole grows at an accelerating rate (a plot of numbers against time sweeps upwards), because the population growth rate is a product of the individual rate (constant) and the accelerating number of individuals. In Chapter 5, such exponential growth was contrasted with a population limited by intraspecific competition (such as one described by the ‘logistic’ equation), where the rate of increase per individual *decreases* as population size increases. In the case of the global human population

past population growth: ‘more than exponential’



## 12.1 TOPICAL ECONCERNS

### 12.1 Topical ECONcerns

#### The human population problem

What is 'the human population problem'? This is not an easy question to pin down, but what follows are some possible versions of the answer (Cohen, 1995, 2003, 2005). The real problem, of course, may be a combination of these – or of these and others. There is little doubt, though, that there *is* a problem, and that the problem is 'ours', collectively.

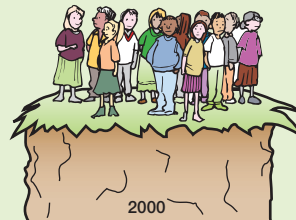
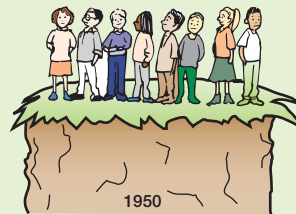
- *The present size of the global human population is unsustainably high.* Around AD 200, when there were about a quarter of a billion people on Earth, Quintus Septimius Florens Tertullianus wrote that 'we are burdensome to the world, the resources are scarcely adequate to us'. By 2005 the total had risen to an estimated 6.5 billion (United Nations 2005).



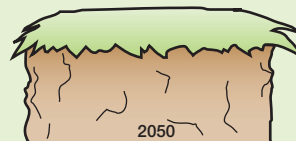
- *It is not the size but the distribution over the Earth of the human population that is unsustainable.* The fraction of the population living, highly concentrated, in an urban environment has risen from around 3% in 1800 to 29% in 1950 and 47% in 2000. Each agricultural worker today has to feed her- or himself plus one city dweller; by 2050 that will have risen to two urbanites (Cohen 2005).



- *The present rate of growth in size of the global human population is unsustainably high.* Prior to the widespread agricultural revolution of the 18th century, the human population, very roughly, had taken 1000 years to double in size. The most recent doubling took just 39 years (Cohen 2001).



?!



- *It is not the size but the age distribution of the global human population that is unsustainable.* In the 'developed' regions of the world, the percentage of the population that was elderly (over 65) rose from 7.6% in 1950 to 12.1% in 1990. This proportion will jump dramatically after 2010 when the large cohorts born after World War II pass 65.



- *It is not the size but the uneven distribution of resources within the global population that is unsustainable.* In 1992, the 830 million people of the world's richest countries enjoyed an average income equivalent to US\$22,000 per annum. The 2.6 billion people in the middle income countries received \$1600. But the 2 billion in the poorest countries got just \$400. These averages themselves hide enormous inequalities.

- 1 What role or responsibility does the individual, as opposed to government, have in responding to the human population problem?
- 2 Which of the variants of the problem, above, pose particular questions of the relationship between the developed and the developing parts of the world or between the 'haves' and the 'have nots'?



(Box 12.2), however, the rate of increase per individual (and also therefore the annual percentage increase in size: the rate of increase per 100 individuals) has certainly not been decreasing – but neither has it remained constant (Cohen, 1995). Rather, the individual rate has itself been accelerating. Even exponential growth would be unsustainable; but the more-than-exponential growth that we have witnessed would, if continued, become unsustainable even sooner.



## 12.2 Quantitative aspects

### 12.2 QUANTITATIVE ASPECTS

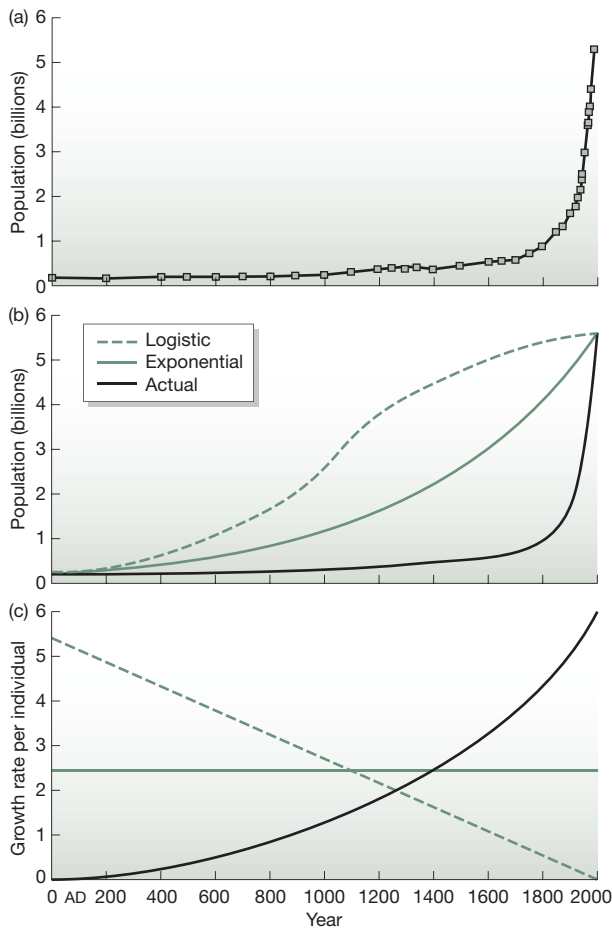
#### The growth of human populations

Figure 12.1 shows estimates of the size of the global human population from 2000 years ago to the present. Apart from the occasional hesitation and even rarer downturn (such as that caused by the ravages of the Black Death towards the end of the 14th century) the overall picture has clearly been one of ever more rapid population growth: the slope of the curve gets steeper and steeper.

But is this exponential growth? The answer is a conclusive 'No'. Figure 12.1b shows this same graph

(black line), but also shows: (i) what an exponentially growing population would have looked like that started at the same point 2000 years ago and finished at the present population size; and (ii) for the sake of contrast, a population anchored at the same start and finish points but growing according to the logistic equation.

Disregarding the logistic as utterly unrealistic, it is also clear that exponential growth is much more 'gradual' than what has actually been observed. The crux of the difference between these three graphs is

**Figure 12.1**

See text for details.

shown in Figure 12.1c, which uses the same information, but this time plots the changing *growth rate per individual* against time: the *per capita* rate. This parameter was introduced in Box 5.4, where it was described, formally, as  $dN/dt \cdot (1/N)$  or, in words, as the rate of population growth,  $dN/dt$ , divided by the number of individuals. For the logistic, under the influence of increasingly intense intraspecific competition, the

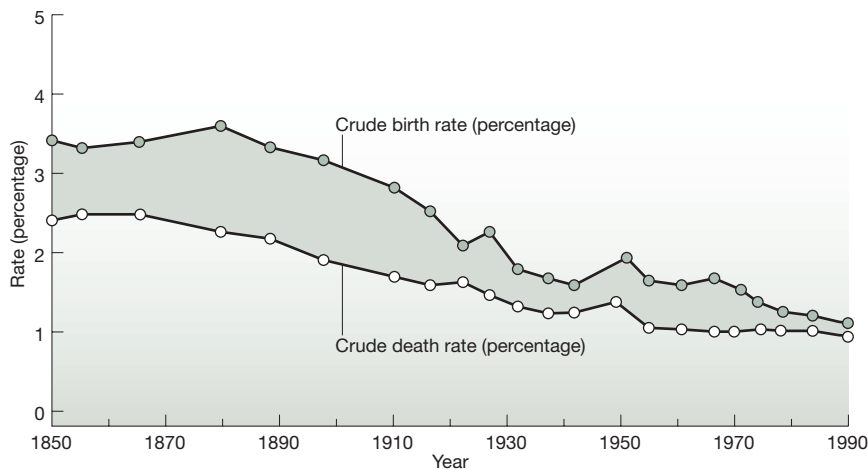
growth rate per individual declines in a straight line down to zero – as it always does for the logistic. For exponential growth, the rate is constant – again ‘by definition’. But the actual growth curve gives rise to an individual rate which not only increases with time as the global population has increased – it increases more than linearly – it accelerates. The historical pattern of growth has been more than exponential.

### 12.2.3 Predicting the future

prediction is more than projection

It is interesting to see what has happened to the total human population in the past – and to do so alerts us to the scale of the problem we face – but the major practical importance of such a survey lies in the opportunity it might provide to

AFTER COHEN, 1995

**Figure 12.2**

The decline in the annual rate of population growth in Europe since 1850 has been associated with a decline in the death rate, followed by a decline in the birth rate, and an overall narrowing of the gap between the two.

predict future population sizes and rates of growth. There is an enormous difference, however, between projection and prediction. Simply to project forwards would be to make the almost certainly false assumption that things will go on in the future just as they have in the past.

Prediction, by contrast, requires an *understanding* of what has happened in the past, as well as how the present differs from the past, and finally how these differences might translate into future patterns of population growth. In particular, it is essential to recognize that the global population of humans is a collection of smaller populations, each with its own often very different characteristics. Like all ecological populations, the human population is heterogeneous.

One common way in which subpopulations have been distinguished has been in terms of the ‘demographic transition’. Three groups of nations can be recognized: those that passed through the demographic transition ‘early’ (pre-1945), ‘late’ (since 1945) or ‘not yet’ (pre-transition countries). The pattern, illustrated for the combined ‘early transition’ populations of Europe in Figure 12.2, is as follows. Initially, both the birth rate and the death rate are high, but the former is only slightly greater than the latter, so the overall rate of population increase is only moderate or small. (This is presumed to have been the case in all human populations at some time in the past.) Next, the death rate declines while the birth rate remains high, so the population growth rate increases. Subsequently, however, the birth rate also declines until it is similar to or perhaps even lower than the death rate. The population growth rate therefore declines again eventually (sometimes to become negative with the death rate higher than the birth rate), though at a population size far greater than before the transition began.

The hypothesis commonly proposed to explain this transition, put simply, is that it is an inevitable consequence of industrialization, education and general modernization leading, first, through medical advances, to the drop in death rates, and then, through the choices people make (delaying having children and so on) to the drop in birth rates.

Certainly, when all the regional populations of the world are considered together, there has been a dramatic decline from the peak population growth rate of about 2.1% per year in 1965–1970 to around 1.1–1.2% per year today (Figure 12.3). And, as Cohen (2005) points out, while population growth rate has

the global population is heterogeneous

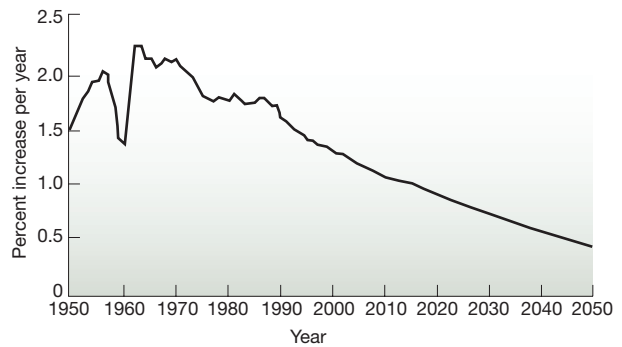
early, late and future demographic transitions

global population growth rate peaked before 1970 and has declined since then



**Figure 12.3**

Population growth rate averaged for the world as a whole from 1950 to 2050.



AFTER COHEN 2001. BASED ON U.S. CENSUS BUREAU DATA

the current decade is unique in the history of human population dynamics

fallen at times in the past (during the plague and great wars), never before the 20th century has a fall in the global population growth rate been 'voluntary'.

The decade we are now passing through (2000–2010) has a very special place in human history because it will encompass three unique transitions:

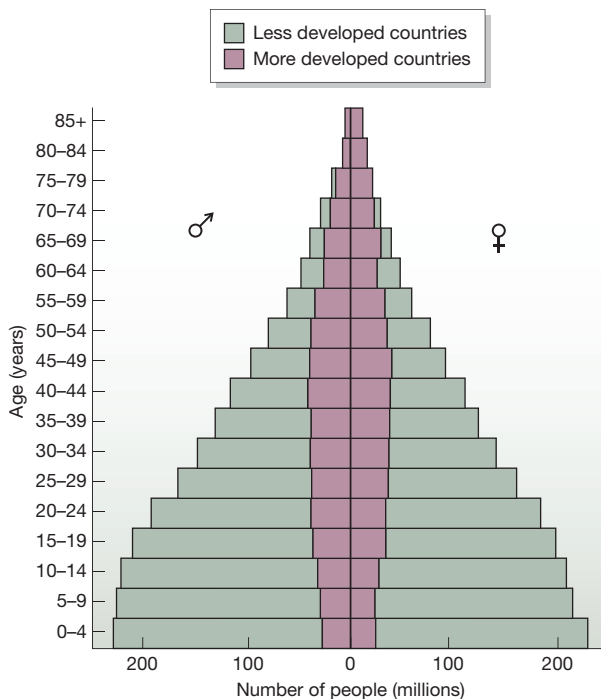
- 1 Until now, young people (e.g. the 0–4 years class) have always outnumbered old people (e.g. the 60+ years class), but from 2000 the old will outnumber the young.
- 2 Until now, rural people have always outnumbered urban people, but from approximately 2007 urban people will predominate.
- 3 From 2003 onward, women, on average, worldwide have had, and will continue to have, too few or just enough children during their lifetime to replace themselves and the children's father in the next generation (Cohen 2005).

The first two transitions must be considered problematic from the point of view of sustainability – will the small population of workers be able to sustain a large body of senior citizens? And will the small population of agricultural workers be able to provide food for the rest of us? The third transition gives cause for some optimism – but the dramatic drop in population growth rate by no means provides an immediate fix to the population problem, as we will see in the next section.

### 12.2.4 Two future inevitabilities

unsustainable age structures?

Even if it were possible to effect some kind of demographic transition in all countries of the world, so that the birth rates were no more than the death rates (zero growth), would the 'population problem' be solved? The answer, sadly, is 'No', for at least two important reasons. First, there is a big difference in age structure between a population with equal birth and death rates in which both those rates are high and one in which both are low. When life tables were described in Chapter 5, we made the point that the net reproductive rate of a population was a reflection of the age-related patterns of survival and birth. A given net reproductive rate, though, can be arrived at through a literally infinite number of different birth and death patterns, and these different combinations themselves give rise to different age structures within the population. If birth rates are

**Figure 12.4**

Predicted population size and age structure in 2050 for the less developed and more developed countries of the world. The horizontal scale is in millions of people (males to the left and females to the right), and the vertical scale shows age groups in 5-year increments. In the two centuries prior to 1950, Europe and the New World experienced the most rapid population growth, while the populations of most of Asia and Africa grew very slowly. But since 1950, rapid population growth has shifted from Western countries to Africa, the Middle East and Asia. Note the way the population of more developed countries becomes strongly biased towards older people, while that of less developed countries demonstrates a very much stronger representation of young people. China and the USA are excluded from the graph because they are exceptions in their categories: China's long-standing one-child policy will produce an age structure more like developed countries and the USA will retain a 'younger' age profile because of substantial immigration.

high but survival rates low ('pre-transition') then there will be many young, and relatively few old individuals in the population. But if birth rates are low and survival rates high – the 'ideal' to which we might aspire 'post-transition' – then relatively few young, productive individuals will be called upon to support the many who are old, unproductive and dependent (see Box 12.1). The size and growth rates of the human population are not the only problems: the age structure of a population adds yet another (Figure 12.4).

Moreover, suppose that our understanding was so sophisticated, and our power so complete, that we could establish equal birth and death rates tomorrow. Would the human population stop growing? The answer, once again, is 'No'. Population growth has its own momentum, which would still have to be contended with. Even with a birth rate matched to the death rate, there would be many years before a stable age structure was established, and in the mean time there would be considerable further population growth before numbers leveled off. According to a population projection prepared by the United Nations (the 'medium fertility variant'), the world's population is expected to grow from 6.3 billion today to peak at 8.9 billion in 2050 (Cohen, 2003). The reason, simply, is that there are, for example, many more babies in the world now than there were 25 years ago, and so even if birth rate per capita drops considerably now, there will still be many more births in 25 years' time, when these babies grow up, than at present; and these children, in turn, will continue the momentum effect before an approximately stable age structure is eventually established. As can be gauged from Figure 12.4 it is the populations in the developing regions of the world, dominated by young individuals, that will provide most of the momentum for further population growth.

the momentum of population growth

### 12.2.5 A global carrying capacity?

The current rate of increase in the size of the global population is unsustainable even though it is lower now than it has been: in a finite space and with finite resources, no population can continue to grow forever. What is an appropriate response to this? To suggest an answer, it is necessary to have some sense of a target, and thus it is interesting, and may be important, to know how large a population of humans could be sustained on the Earth. What is the global carrying capacity?

There is astonishing variation in the estimates that have been proposed over the last 300 or so years and even the estimates since 1970 span three orders of magnitude – from 1 to 1000 billion. To illustrate the difficulty in arriving at an estimate of global carrying capacity, a few examples are described here (see Cohen, 1995, 2005 for further details of the authors mentioned below).

some estimates of 'the global carrying capacity'

In 1679, van Leeuwenhoek estimated that the inhabited area of the Earth was 13,385 times larger than his home nation of Holland, whose population then was about 1 million people. He then assumed that all this area could be populated as densely as Holland, yielding an upper limit of roughly 13.4 billion.

In 1967, De Wit asked the question 'How many people can live on Earth if photosynthesis is the limiting process?' The answer he arrived at was roughly 1000 billion. He built into his calculation the fact that the length of the potential growing season varies with latitude, but assumed, amongst other things, that neither water nor minerals were limiting. He acknowledged that if people wanted to eat meat, or wanted what most of us consider a reasonable amount of living space, and so on, then the estimate would be much less.

By contrast, Hulett in 1970 assumed that levels of affluence and consumption in the United States were 'optimal' for the whole world, and that not only food but requirements for renewable resources like wood and non-renewable resources like steel and aluminum needed to be brought into the calculations. The figure he came up with was no more than 1 billion. Kates and others, in a series of reports from 1988, made similar assumptions but worked from global rather than United States averages and estimated a global carrying capacity of 5.9 billion people on a basic diet (principally vegetarian), or 3.9 billion on an 'improved' diet (about 15% of calories from animal products) or 2.9 billion on a diet with 25% of calories from animal products.

More recently, Wackernagel and his colleagues in 2002 sought to quantify the amount of land humans use to supply resources and to absorb wastes (embodied in their 'ecological footprint' concept). Their preliminary assessment was that people were using 70% of the biosphere's capacity in 1961 and 120% by 1999. They reasoned, in other words, that global carrying capacity was exceeded before the turn of the millennium – when our population was about 6 billion.

defining global carrying capacity is far from straightforward

As Cohen (2005) has pointed out, many estimates have been based on (or rely heavily on) a single dimension – biologically productive land area, water, energy, food and so on – and a difficulty with them all is the reality that the impact of one factor depends on the value of others. Thus, for example, if water is scarce and energy is abundant, water can be desalinated and transported to where it is in short supply, a solution that is not available if energy is expensive. Moreover, it is clear from the examples above that there is a difference between the number the Earth can support and the number that can be supported with an

acceptable standard of living. The higher estimates come closer to the concept of a carrying capacity we normally apply to other organisms (see Chapter 5) – a number ‘imposed’ by the limiting resources of the environment. But it is unlikely that many of us would choose to live crushed up against an environmental ceiling or wish it on our descendants.

In any case, it is a big step to assume that the human population is limited ‘from below’ by its resources rather than ‘from above’ by its natural enemies. Infectious disease in particular, which not long ago was considered to be an enemy largely vanquished, is now once again perceived, for example by the World Health Organization, as a major threat to human welfare. Just consider the growing epidemics in tuberculosis and HIV and AIDS and the deaths caused by malaria. We saw in Chapter 7 that many infectious diseases thrive best in the densest populations.

Any suggestions we make about a global carrying capacity clearly depend on choices we make both for ourselves and for others. Most of us would choose to live at least as well as we do at present, but can the global population afford to choose for the whole world to live at least as well as those in developed countries do now? The answer to any question depends on what is meant by the question – defining what we mean by ‘the global carrying capacity’ is far from straightforward.

## 12.3 Harvesting living resources from the wild

A major limit to the number of people the Earth can support is the food that can be obtained. Populations of many species living freely in the wild are exploited for food by humans, who ‘cull’ or ‘harvest’ a proportion of the population, leaving some individuals behind to grow and reproduce for future harvests. Primitive human societies obtained all their resources like this, by hunting and gathering from nature, and humans continue to garner some resources in this way. The resources may be fish from the sea, deer from a moorland or timber from a forest. There is an important difference between resources obtained in this way and those that are farmed (Sections 12.4 and 12.6). Farmed resources are obtained by taking chosen species of plant or animal, domesticating them (often changing them genetically) and growing or rearing them in more or less controlled monocultures. These resources tend to be owned and managed by a farmer or organization. In contrast, most of the oceans and forests that are fished and hunted have at one time been common property, open to free-for-all unsustainable looting by all-comers. Recently, though, fishing and hunting have also come under increasing national and international regulation and national claims to ‘ownership’. Many of our examples in this section are of fish or fisheries, but the principles apply to the harvesting of any natural resource.

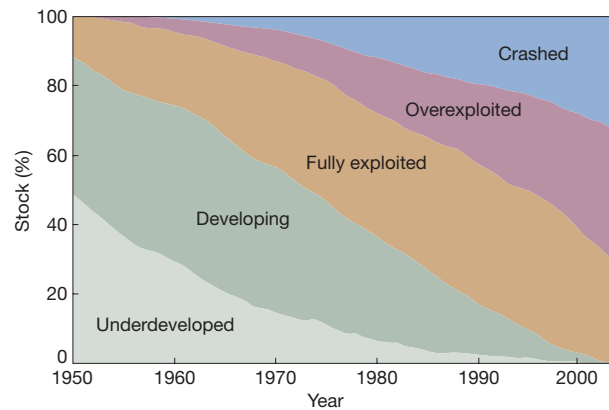
### 12.3.1 Fisheries: maximum sustainable yields

Whenever a natural population is exploited there is a risk of overexploitation: too many individuals are removed and the population is driven into biological jeopardy or economic insignificance – perhaps even to extinction. Global catches of marine fish rose five-fold between 1950 and 1989 and many of the world’s fish

aiming for the narrow path  
between over- and  
underexploitation

### Figure 12.5

Changes in the contribution to global marine fish production made by fisheries in different phases of their exploitation. In the 1950s most of the catches were from undeveloped fisheries, but by 2000 most fisheries were fully exploited (near their maximum sustainable yield), or overexploited or had already collapsed.



AFTER KHAN ET AL., 2006

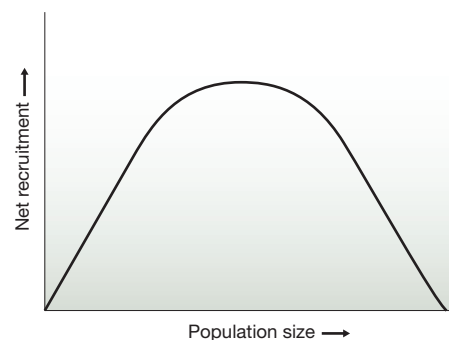
stocks are now beyond the point of overexploitation (Figure 12.5). But harvesters also want to avoid underexploitation: if fewer individuals are removed than the population can bear, the harvested crop is smaller than necessary, potential consumers are deprived and those who do the harvesting are underemployed. It is not easy to tread the narrow path between under- and overexploitation. It is asking a great deal of a management policy to combine the well-being of the exploited species, the profitability of the harvesting enterprise, continuing employment for the workforce and the maintenance of traditional lifestyles, social customs and natural biodiversity.

The most fundamental aspects of ecology that we need to understand here were introduced in Chapter 5 when the effects of intraspecific competition on populations were discussed. To determine the best way to exploit a population, it is necessary to know what the consequences will be of different exploitation 'strategies'. But in order to know these consequences, we first need some understanding of the dynamics of the population in the absence of, or prior to, exploitation. It is usual to assume that, before it is exploited, a harvestable population is crowded and intraspecific competition is intense. Summarizing from Chapter 5, and remembering that these are broad generalizations:

- populations in the absence of exploitation can be expected to settle around their carrying capacity, but exploitation will reduce numbers to less than this;
- exploitation, by reducing the intensity of competition, moves the population 'leftwards' along the humped net recruitment curve, increasing the net number of recruits to the population per unit time (Figure 12.6).

### Figure 12.6

The humped relationship between the net recruitment into a population (births minus deaths) and the size of that population, resulting from the effects of intraspecific competition (see Chapter 5). Population size increases from left to right, but increasing rates of exploitation take the population from right to left.



population dynamics in the absence of exploitation – humped net recruitment curves

In fact, we can go further with Figure 12.6, since it is clear from the shape of the curve that there must be an ‘intermediate’ population size at which the rate of net recruitment is highest. Consider a time scale of years. The peak of the curve might be ‘10 million new fish recruited each year’. This is then also the highest number of new fish that could be removed from the population each year that the population itself could replenish. It is known as the *maximum sustainable yield* (MSY): the largest harvest that can be removed from the population regularly and indefinitely. It looks as though a fishery could tread the narrow path between under- and overexploitation if the fishers could find a way to achieve this MSY.

The MSY concept has been the guiding principle in resource management for many years in fisheries, forestry and wildlife exploitation, but it is very far from being the perfect answer for a variety of reasons.

- 1 By treating the population as a number of similar individuals, it ignores all aspects of population structure such as size or age classes and their differential rates of growth, survival and reproduction.
- 2 By being based on a single recruitment curve, it treats the environment as unvarying.
- 3 In practice, it may be impossible to obtain a reliable estimate of the MSY.
- 4 Achieving an MSY is by no means the only, nor necessarily the best, criterion by which success in the management of a harvesting operation should be judged. (It may, for example, be more important to provide stable, long-term employment for the workforce.)

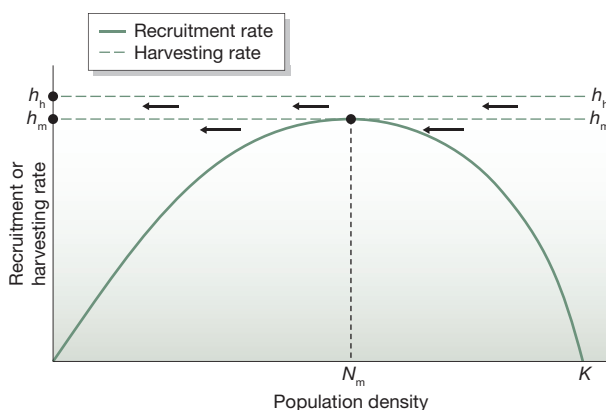
MSY – the narrow path?

the MSY concept has shortcomings

### 12.3.2 Obtaining MSYs through fixed quotas

There are two simple ways of obtaining an MSY on a regular basis: through a ‘fixed quota’ and through a ‘fixed effort’. With fixed quota MSY harvesting (Figure 12.7), the same amount, the MSY, is removed from the population every year. If (and it is a big if) the population stayed exactly at the peak of its net recruitment curve, then this could work: each year the members of the population, through their own growth and reproduction, would add exactly what the harvesting removed. But if by chance numbers fell even slightly below those at which the curve peaked, then the numbers harvested would exceed those recruited. Population size would then decline to below the peak of the curve,

the fragility of fixed quota harvesting . . .

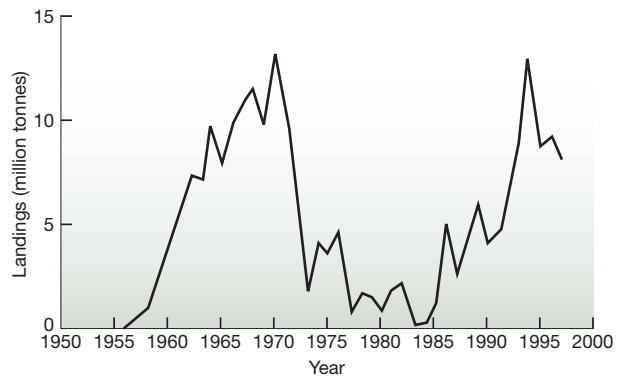


**Figure 12.7**

Fixed quota harvesting. The figure shows a single recruitment curve (solid line; recruitment in relation to density,  $N$ ) and two fixed quota harvesting curves (dashed lines): high quota ( $h_h$ ), and MSY quota ( $h_m$ ). The arrows in the figure refer to changes to be expected in abundance under the influence of the harvesting rate to which the arrows are closest. The black dots indicate equilibria. At  $h_h$  the only ‘equilibrium’ is when the population is driven to extinction. The MSY is obtained at  $h_m$  because it just touches the peak of the recruitment curve (at a density  $N_m$ ): populations greater than  $N_m$  are reduced to  $N_m$ , but populations smaller than  $N_m$  are driven to extinction.  $K$  is the carrying capacity, the density where the population is expected to settle in the absence of exploitation.

### Figure 12.8

Landings of the Peruvian anchovy since 1950. Note the dramatic crash that resulted mainly as a result of overfishing. The stock has taken 20 years to rebuild.



AFTER JENNINGS ET AL., 2001

and if a fixed quota at the MSY level were maintained the population would carry on declining until it was extinct (Figure 12.7). Furthermore, if the MSY was even slightly overestimated (and reliable estimates are hard to come by) then harvesting rate would always exceed the recruitment rate and extinction would again follow. In short, a fixed quota at the MSY level might be desirable and reasonable in a wholly predictable world about which we had perfect knowledge. But in the real world of fluctuating environments and imperfect data sets, these fixed quotas are open invitations to disaster.

... borne out in practice

Nevertheless, a fixed quota strategy has frequently been used – a management agency formulates an estimate of the MSY, which is then adopted as the annual quota. On a specified day in the year, the fishery is opened and the accumulated catch is logged. A fairly typical example is provided by the Peruvian anchovy (*Engraulis ringens*) fishery (Figure 12.8). From 1960 to 1972 this was the world's largest single fishery, and it constituted a major sector of the Peruvian economy. Fisheries experts advised that the MSY was around 10 million tonnes annually, and catches were limited accordingly. But the fishing capacity of the fleet expanded, and in 1972 the catch crashed. Overfishing seems, at the least, to have been a major cause of the collapse, although its effects were compounded with the influences of profound environmental fluctuations, discussed below. A moratorium on fishing would have been an ecologically sensible step, but this was not politically feasible: 20,000 people were dependent on the anchovy industry for employment. The Peruvian government therefore allowed fishing to continue. The stock took more than 20 years to recover.

### 12.3.3 Obtaining MSYs through fixed effort

relative robustness of fixed effort harvesting

An alternative to trying to maintain a constant harvest is to maintain a constant 'harvesting effort' (e.g. the number of 'trawler-days' in a fishery or the number of 'gun-days' with a hunted population). With such a regime the amount harvested should increase with the size of the population being harvested (Figure 12.9). Now, in contrast to Figure 12.7 if density drops below the peak, new recruitment exceeds the amount harvested and the population recovers. The risk of extinction is much reduced. The disadvantages, however, are first, because there is a fixed effort, the yield varies with population size (there are good, but, more to the point, bad years), and second, steps need to be taken to ensure that nobody makes a greater effort than they are supposed to. Nonetheless, there are many



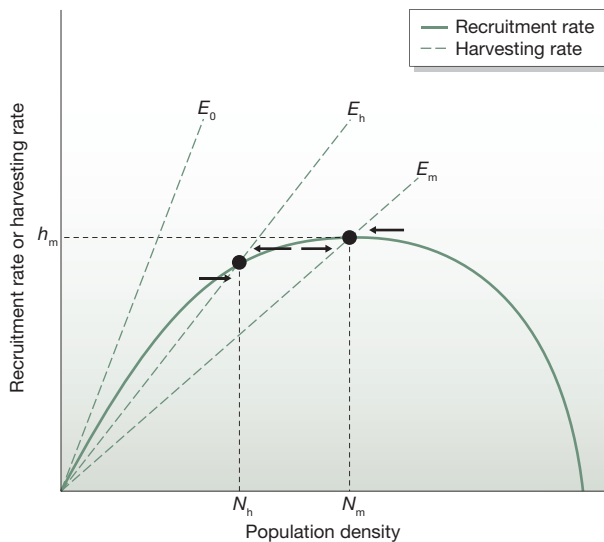


Figure 12.9

Fixed effort harvesting. Curves, arrows and dots as in Figure 12.7. The MSY is obtained with an effort of  $E_m$ , leading to a stable equilibrium at a density of  $N_m$  with a yield of  $h_m$ . At a somewhat higher effort ( $E_h$ ), the equilibrium density and the yield are both lower than with  $E_m$ , but the equilibrium is still stable. Only at a much higher effort ( $E_0$ ) is the population driven to extinction.

examples of harvests being managed by legislative regulation of effort. Harvesting of the important Pacific halibut (*Hippoglossus stenolepis*), for example, is limited by seasonal closures and sanctuary zones, though heavy investment in fisheries protection vessels is needed to control law breakers.

### 12.3.4 Beyond MSYs

There is no doubt that fishing pressure often exerts a great strain on populations. But the collapse of fish stocks in one year rather than any other is often the result of an occurrence of unusually unfavorable environmental conditions, rather than simply overfishing.

Harvests of the Peruvian anchovy (see Figure 12.8) collapsed from 1972 to 1973, but a previous steady rise in catches had already dipped in the mid-1960s as a result of an El Niño event: this happens when warm tropical water from the north reduces the upwelling, and hence the productivity, of the nutrient-rich cold Peruvian current coming from the south. By 1973, however, commercial fishing had so greatly increased that the subsequent El Niño event had even more severe consequences. There were some signs of recovery from 1973 to 1982, but a further collapse occurred in 1983 associated with yet another El Niño event. It is unlikely that the El Niño events would have had such severe effects if the anchovy had only been lightly fished. It is equally clear, though, that the history of the Peruvian anchovy fishery cannot be explained simply in terms of overfishing.

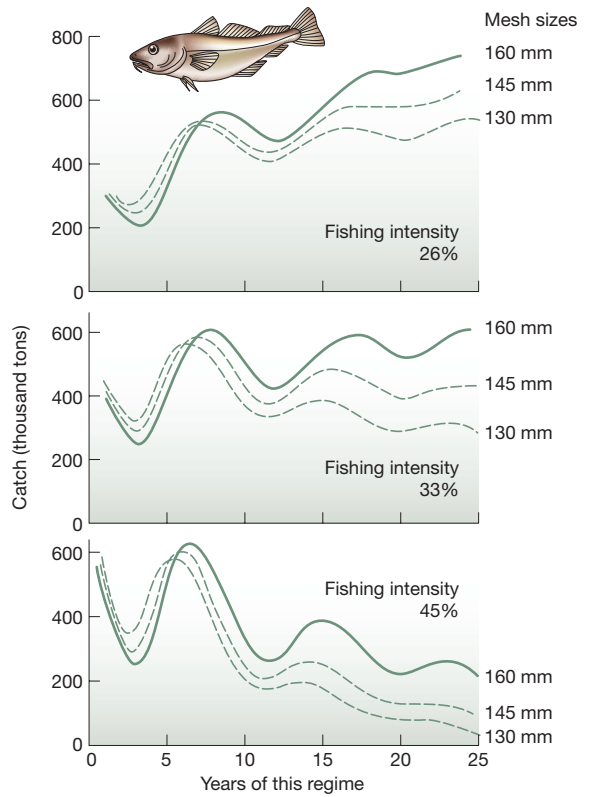
So far, this account has ignored population structure of the exploited species. This is a bad fault for two reasons. First, most harvesting practices are primarily interested in only a portion of the harvested population (mature trees, fish that are large enough to be saleable, etc.). Second, ‘recruitment’ is, in practice, a complex process incorporating adult survival, adult fecundity, juvenile survival, juvenile growth and so on, each of which may respond in its own way to changes in density and harvesting strategy. An example of a model that takes some of these variables into account was that developed for the Arcto-Norwegian cod fishery, the most northerly fish stock in the Atlantic Ocean. The numbers of fish

environmental fluctuations – the anchovy and El Niño

population structure and the Arctic cod (*Gadus morhua*)

**Figure 12.10**

Predictions for the stock of Arctic cod under three intensities of fishing and three different sizes of mesh in the nets. Larger meshes allow more and larger fish to escape capture. The largest effort (45%, bottom panel) is clearly unsustainable, regardless of the mesh size used. The largest sustainable catches are achieved with a low fishing effort (26%, upper panel) and a large mesh size.



AFTER PITCHER &amp; HART, 1982

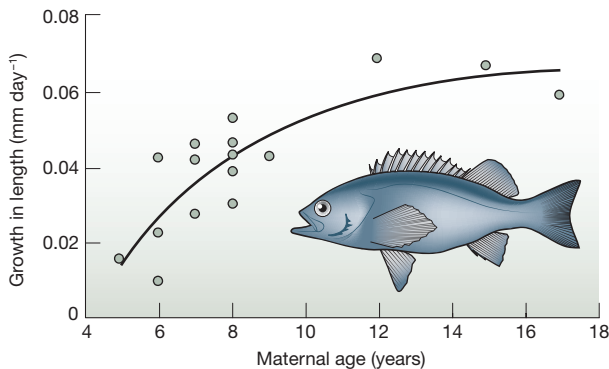
in different age classes were known for the late 1960s and this information was used to predict the tonnage of fish likely to be caught with different intensities of harvesting and with different net mesh sizes. The model predicted that the long-term prospects for the fishery were best ensured with a low intensity of fishing (less than 30%) and a large mesh size. These gave the fish more opportunity to grow and reproduce before they were caught (Figure 12.10). The recommendations from the model were ignored and, as predicted, the stocks of cod fell disastrously.

Indigenous harvesters have long had their own ‘regulations’ to reduce the chance of overexploitation. In their harvesting of moi (*Polydactylus sexfilis*), Hawaiian fishermen, using traditional methods along the shore, take only intermediate-sized fishes, leaving both juveniles and large females. Thus they go a stage further than simply increasing net mesh size, which, while reducing the numbers of smaller individuals taken, nevertheless captures the largest individuals in the population. The good sense of the Hawaiian strategy has been reinforced by the discovery that large females of some fish not only produce exponentially more offspring but also that each of their offspring grows faster (Figure 12.11) and is more likely to reach adulthood. Protecting the largest individuals may give a great boost to sustainability.

Managing most marine fisheries to achieve perfect, optimum yields is an unattainable dream. There are generally too few researchers to do the work and, in many parts of the world, no researchers at all. In these situations, a precautionary approach to fisheries management might involve locking away a proportion of a coastal or coral community in marine-protected areas (Hall, 1998). The term

a strategy of taking only intermediate-sized fishes

precautionary management, closed areas and ‘data-less’ management

**Figure 12.11**

The black rockfish (*Sebastes melanops*), off the coast of Oregon, USA, is a long-lived fish that produces live young. Not only do bigger fish produce more eggs to be fertilized, but the proportion of these that are in fact fertilized is itself greater in larger females. Furthermore, as shown in the graph, larvae produced by older (larger) females grow more than three times as fast as do larvae produced by their younger (smaller) counterparts.

*data-less management* has been applied to situations where local villagers follow simple prescriptions to make sustainability more likely – for example locals on the Pacific island of Vanuatu were provided with some simple principles of management for their trochus (*Tectus niloticus*) shellfishery: stocks should be harvested every 3 years and left unfished in between. The outcome has apparently been successful: continued economic viability (Johannes, 1998).

## 12.4 The farming of monocultures

Globally there is abundant food. Between 1961 and 1994 the per capita food supply in developing countries increased by 32% and the proportion of the world's population that was undernourished fell from 35% to 21%, though this is very unevenly distributed. Yet 800 million people remain hungry worldwide, and the rate of increase in per capita food production is falling.

Fishing and hunting (Section 12.3) have been human activities since our early history as hunter-gatherers. But the harvest that can be taken from nature was totally inadequate to support the main phases of growth of human populations. Increasingly, both animals and plants were domesticated and managed in ways that allowed much greater rates of production. The great bulk of the human food resource is now farmed – usually produced as dense populations of single species (*monocultures*). This allows them to be managed in specialized ways that can maximize their productivity, whether as immense monocultures of rice, corn or wheat (Figure 12.12), or as livestock factories producing beef, pork or poultry. Fish, indeed, are increasingly managed in the same way (aquaculture) – reared in enclosures, fed with controlled diets and harvested in mass production. Nearly a quarter of the fish supply in Asia is already produced in this way.

Only monoculture can maximize the rate of food production. This is because it allows the farmer to control and optimize with high precision the density of the populations (livestock or crop plants), the quantity and quality of their resources (food supplied to livestock; fertilizer and water to the crops) and often even the physical conditions of temperature and humidity. With many animals, the monocultures extend to segregating livestock or poultry into narrow age bands or age classes. If the only important criteria are economic ones, then there need be none of the uneconomic mixing of calves with cows or chickens with hens; fish eggs and fry can be segregated from potentially cannibalistic adults; the grossly

monoculture – and beyond

**Figure 12.12**

Agricultural monoculture:  
wheat as far as the eye  
can see.



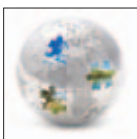
but disease spreads in  
monocultures

uneconomic equality of the sex ratio that is common in nature can be distorted by culling to give efficient all-female dairy herds of cattle, or all-hen populations in batteries for egg production. This is a far cry from the ecology of the primitive human hunter-gatherers, who subsisted on their gleanings from the tangled web of wild nature!

To what extent, though, are modern farming methods sustainable? There is abundant evidence that a high price has to be paid to sustain the high rates of food production achieved by farmed monocultures. For example, they offer ideal conditions for the epidemic spread of diseases such as mastitis, brucellosis and swine fever among livestock and coccidiosis among poultry. Farmed animals are normally kept at densities far higher than their species would meet in nature with the result that disease transmission rates are magnified (see Chapter 7). In addition, high rates of transmission between herds occur as animals are sold from one farming enterprise to another, and it is easy for the farmers themselves, with mud on their boots and their vehicles, to act as vectors of pests and disease. The dramatic spread of foot and mouth disease in 2001 among British livestock provides a graphic example.

Crop plants, too, provide illustrations of the fragility of human dependence on monocultures. The potato, for example, was not introduced across the Atlantic to Europe until the second half of the 16th century, but three centuries later other foods had given way to it, and it had become the almost exclusive food crop of the poorer half of the population of Ireland. Dense monoculture, though, provided ideal conditions for the devastating spread of late blight (the fungal pathogen *Phytophthora infestans*) when it also crossed the Atlantic in the 1840s. The disease spread rapidly, dramatically reducing potato yields and also decomposing the tubers in storage. Out of the Irish population of about 8 million, 1.1 million died in the resulting famine and another 1.5 million emigrated to the UK and the USA.

In more modern history, an outbreak of southern corn leaf blight (caused again by a fungus, *Helminthosporium maydis*) developed in southeastern USA in the late 1960s and spread rapidly after 1970. Most of the corn grown in the area had been derived from the same stock and was genetically almost uniform. This extreme monoculture allowed one specialized race of the pathogen to have devastating consequences. The damage was estimated as at least \$1 billion in the USA and had repercussions on grain prices worldwide. One of our favorite fruits is also at great risk of economic disaster (Box 12.3).



## 12.3 TOPICAL ECONCERNS

### 12.3 Topical ECONcerns

#### Can this fruit be saved? The banana as we know it is on a crash course toward extinction

In June 2005, Dan Koeppel filed the story below.

For nearly everyone in the US, Canada and Europe, a banana is a banana: yellow and sweet, uniformly sized, firmly textured, always seedless.

The Cavendish banana – as the slogan of Chiquita, the globe's largest banana producer, declares – is 'quite possibly the world's perfect food'. . . . It also turns out that the 100 billion Cavendish bananas consumed annually worldwide are perfect from a genetic standpoint, every single one a duplicate of every other. It doesn't matter if it comes from Honduras or Thailand, Jamaica or the Canary Islands – each Cavendish is an identical twin to one first found in Southeast Asia, brought to a Caribbean botanic garden in the early part of the 20th century, and put into commercial production about 50 years ago.

That sameness is the banana's paradox. After 15,000 years of human cultivation, the banana is too perfect, lacking the genetic diversity that is key to species health. What can ail one banana can ail all. A fungus or bacterial disease that infects one plantation could march around the

globe and destroy millions of bunches, leaving supermarket shelves empty.

A wild scenario? Not when you consider that there's already been one banana apocalypse. Until the early 1960s, American cereal bowls and ice cream dishes were filled with the Gros Michel, a banana that was larger and, by all accounts, tastier than the fruit we now eat. Like the Cavendish, the Gros Michel, or 'Big Mike', accounted for nearly all the sales of sweet bananas in the Americas and Europe. But starting in the early part of the last century, a fungus called Panama disease began infecting the Big Mike harvest.

(All content © 2005 Popular Science. A Time4 Media Company. All rights reserved. Reproduction in whole or in part without permission is prohibited.)

- 1 Use a web search to discover the options that might be used to safeguard the banana industry.
- 2 How far fetched do you consider the risk of global economic terrorism by deliberate spread of a banana disease?

#### 12.4.1 Degradation and erosion of soil

A United Nations report (1998) stated:

Agricultural intensification in recent decades has taken a heavy toll on the environment. Poor cultivation and irrigation techniques and excessive use of pesticides and herbicides have led to widespread soil degradation and water contamination.

Around 300 million hectares are now severely degraded around the world and a further 1.2 billion hectares – 10% of the Earth's vegetated surface – can be described as moderately degraded. Clearly much of agricultural practice has not been sustainable.

Land without soil can support only very small primitive plants such as lichens and mosses that can cling onto a rock surface. The rest of the world's terrestrial

agriculture and forestry  
requires soil

soil forms . . . and is lost

vegetation has to be rooted in soil, which gives it physical support. The soil also serves as a store of essential mineral nutrients and water that are extracted by the roots during plant growth. Soil develops by the accumulation of finely divided mineral products of rock weathering and decomposing organic residues from previous vegetation. The characteristics of the soil under natural vegetation in any particular climatic region and on any particular rock type depends on the balance between these processes of accumulation and forces that degrade and remove the soil.

The formation and persistence of soil in a region depend on local natural checks and balances. Soil may be lost by being washed or blown away, perhaps to be redeposited as an accumulation of fine-textured 'loess' somewhere else. Soil is best protected when it contains organic matter, is always wholly covered with vegetation, is finely interwoven with roots and rootlets and is on horizontal ground. Natural soil systems are probably *always* too fragile to be fully sustained when land is brought into cultivation. Dramatic evidence of unsustainable land use came from the 'dust bowl' disaster in the Great Plains of the United States and a similar disaster happening currently in China (Box 12.4).



## 12.4 Historical landmarks

### 12.4 HISTORICAL LANDMARKS

#### Soil erosion, America's historical 'dust bowl' and China's current problem

Large areas of southeastern Colorado, southwestern Kansas and parts of Texas, Oklahoma and north-eastern New Mexico were once used to support rangeland management of livestock. The vegetation consisted largely of native perennial grasses and had been neither ploughed nor sown with seed.

At the time of the First World War, much of the land was ploughed and annual crops of wheat were grown. There were poor crops in the early 1930s due to severe drought and the topsoil was exposed and carried away by the wind. Black blizzards of windblown soil blocked out the sun and piled the dirt in drifts. Occasionally the dust storms swept completely across the country to the East Coast. Thousands of families were forced to leave the region at the height of the Great Depression in the early and mid-1930s. The wind erosion was gradually halted with federal aid: windbreaks were planted and much of the grassland was restored. By the early 1940s the area had largely recovered.

The story is being repeated today in northwest China, where the need to feed 1.3 billion people has

led to the raising of too many cattle and sheep, and the use of too many plows. This is more than the land can stand and 2300 km<sup>2</sup> are turning to desert each year. A huge dust storm blanketed areas from Canada to Arizona in April 2001 – the dust originated in China.



Dust bowl field and abandoned farm.

© VISUALS UNLIMITED



In an ideal sustainable world, new soil would be formed as fast as the old was lost. In Britain about 0.2 tonnes of new soil is produced naturally per hectare per year and it has been suggested that a tolerable (although not necessarily sustainable) rate of soil erosion might be about  $2.0 \text{ t ha}^{-1} \text{ yr}^{-1}$ . However, rates of erosion have been recorded of up to  $48 \text{ t ha}^{-1} \text{ yr}^{-1}$ !

Almost all (perhaps all) agricultural land will support higher yields if artificial fertilizers are applied to supplement the nitrogen, phosphorus and potassium supplied naturally by the soil. Fertilizers are cheap, easy to handle, of a guaranteed composition, allow even and accurate application, and higher and more predictable yields. When there is an overwhelming reliance on them, however, maintaining the organic matter capital of the soil tends to be neglected and has declined everywhere.

The degradation of soil by agriculture can be prevented, or at least slowed down, by: (i) incorporating farmyard manure, crop residues and animal wastes; (ii) alternating years under cultivation with years of fallow; or (iii) returning the land to grazed pasture or rangeland. Such practices conserve soil quality in technologically sophisticated agricultures in temperate regions.

But soil degradation is most serious and least easily prevented in less developed countries. The problems are greatest in high rainfall areas and on steeply sloping ground in the tropics where organic matter in the soil also decomposes more rapidly. The United Nations soil conservation strategy of 'Agenda 21' (formulated in Rio de Janeiro, 1992) recommended measures to prevent soil erosion and promote erosion control.

The most cost-effective technology used in reducing soil erosion is considered to be contour-based cultivation (Figure 12.13). In India, contour ditches have helped to quadruple the survival chances of tree seedlings and quintuple their early growth in height. Deeply rooted, hedge-forming 'vetiver' grass, planted in contour strips across hill slopes, slows water runoff dramatically, reduces erosion and increases the moisture available for crop growth. Currently 90% of soil conservation efforts in India are based on such biological systems. Simple technologies involving rock embankments constructed along contour lines for soil and water conservation have also been successful. Embanked fields in Burkina Faso (west Africa) yielded an average of 10% more crop production than traditional fields in a normal year and, in drier years, almost 50% more (United Nations, 1998).

soil maintenance

contour plowing and terracing –  
Agenda 21**Figure 12.13**

Terracing of hill and mountainous land.



Such terracing provides a very high level of soil conservation but is possible only where labor is cheap. On lesser slopes, by ploughing and cultivating in strips along the contours, runoff of soil can be significantly reduced.

desertization and salinization

Agricultural land is also highly susceptible to degradation in arid and semiarid regions. Both overgrazing and excessive cultivation expose the soil directly to erosion by the wind and to rare but fierce rainstorms. In the process of '*desertization*', land that is arid or semiarid but has supported subsistence or nomadic agriculture gives way to desert. The process has often been slowed down for a time by irrigating the land. This gives a temporary remission but lowers the water table and salts accumulate in the topsoil (*salinization*). Once salts have started to accumulate, the process of salinization tends to spread and leads to an expansion of sterile, white salt deserts. This has been a particular hazard in irrigated areas of Pakistan.

forests protect . . . but not if harvested by clear felling

Forests protect soil from erosion because the canopy absorbs the direct impact of the rain on the soil surface, the perennial root systems bind the soil and leaf fall continually adds organic matter. But when forests are clear felled and then replanted, there is an open 'window of opportunity' for soil erosion until the forest canopy closes again. Cultivation and replanting along contours gives some control over soil erosion during this danger period, but the best precaution is to avoid clear felling and extract only a proportion of a forest stand at each harvest. This can often be technically difficult and more expensive.

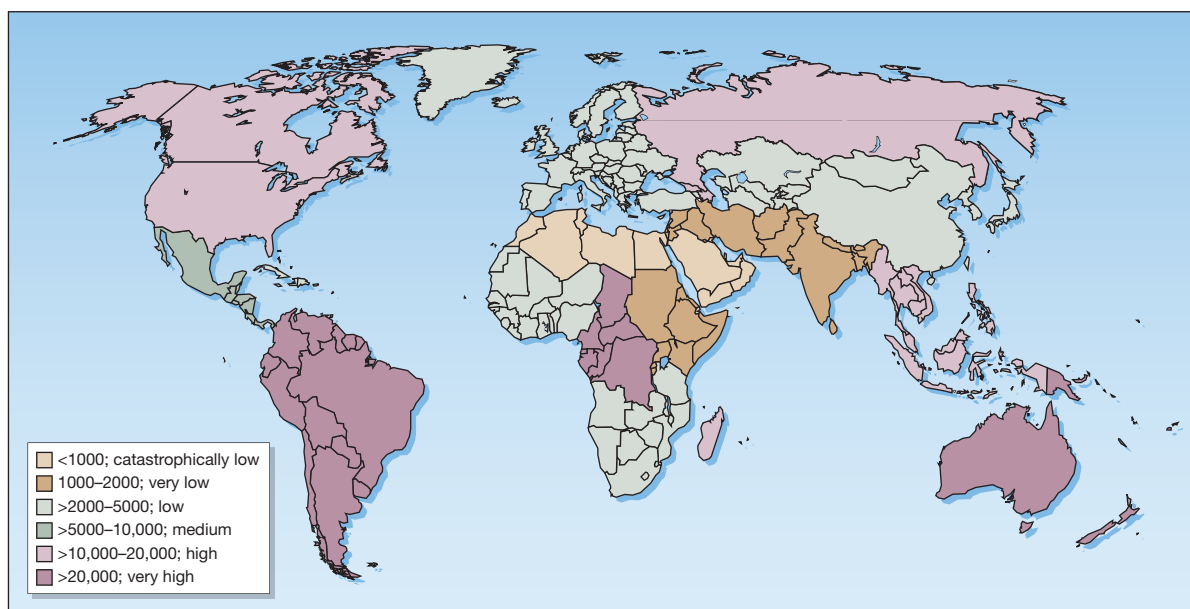
### 12.4.2 The sustainability of water as a resource

water is a finite global resource

In the 1960s and 1970s, the main worry about the sustainability of global resources concerned energy supplies that were recognized to be finite and exhaustible. While energy resources remain finite, concern has shifted because exploration has revealed much larger reserves of oil, gas and even coal than had been entered into earlier environmental balance sheets. Water has now come into sharper focus. Fresh water, which is used in crop irrigation and for domestic consumption, is of crucial importance. On a global scale, agriculture is the largest consumer of fresh water, taking more than 70% of available supplies and more than 90% in parts of South America, central Asia and Africa.

water – the resource that future wars will be fought over?

There is a fixed stock of water on the globe and it is continually recycled as it evaporates from vegetation, land and sea and is then condensed and redistributed as precipitation. The human species now uses, directly or indirectly, more than half of the world's accessible water supply. The fresh water available per capita worldwide fell from 17,000 m<sup>3</sup> in 1950 to 7300 m<sup>3</sup> in 1995 and there is very considerable variation in availability from region to region (Figure 12.14). Many assessments of the problems of water supply suggest that countries with less than 1000 m<sup>3</sup> per person per year experience chronic scarcity. Water is widely thought to be the resource that future wars will be fought over. Even at a national level, the allocation of water resources can cause political problems, as occur for example in conflicts in California between urban and agricultural demands for water from the Colorado River. At the international level, conflict arises between countries that are upstream of their neighbors and are in a position to dam and divert water supplies. There are bitter cross-border disputes in South America, Africa and the Middle East between nations that share river basins.

**Figure 12.14**

Water availability per person from region to region of the globe in 2000. The units are in cubic meters per capita per year.

One response to chronic scarcity of water is to pump it from underground aquifers – but this often happens faster than the aquifers can be recharged. Such activity is clearly unsustainable. It is also the main cause of the loss of land from agriculture due to salinization. The demand for accessible supplies of water for both agriculture and domestic use has led to the plumbing of the Earth's river systems on a vast scale. The number of river dams more than 15 m high increased from about 5000 in 1950 to 38,000 in the 1990s.

In Chapter 13 we discuss the pollution of water by excreta, and by the pesticides and fertilizers applied in agriculture. Water that is uncontaminated by disease agents, nitrates or pesticides is an especially valuable commodity, but contamination occurs all too readily and removing contaminants (e.g. nitrates) is very expensive. Major dams built to control and conserve water in north and west Africa create large bodies of open water in which contamination spreads easily; one consequence has been the rapid spread along rivers of schistosomiasis (a flatworm disease of humans), with infection rates rising from less than 10% to more than 98%.

Maintaining water supplies for human use also creates problems for the conservation of wildlife (see Chapter 14). The waterflow in many of the world's larger rivers is now very heavily controlled – in some cases little water now reaches the sea and wetlands have been lost or are at risk. Moreover, silt accumulates up-river instead of spreading into deltas and flood plains. The results may be catastrophic for wildlife areas and for human communities as well. For example, there is reason to believe that failure of silt deposition in the Nile delta (together with rising sea levels) may cause Egypt to lose up to 19% of its habitable land and displace 16% of its population within 60 years.

contamination and conservation

## 12.5 Pest control

what is a pest?

Pest control is another area in which the sustainability of agricultural practice may be threatened. A pest species is simply one that humans consider undesirable. Estimates suggest that there are around 67,000 species of pests that attack agricultural crops worldwide: 8000 weeds that compete with crops, and 9000 insects and mites and 50,000 plant pathogens that attack them (Pimentel, 1993). Here we consider the sustainability of insect pest control in agriculture to illustrate the types of problems that arise in managed monocultures. We could equally well have chosen the control of weeds or mollusks, or of the pests and diseases of farmed livestock, poultry or fish.

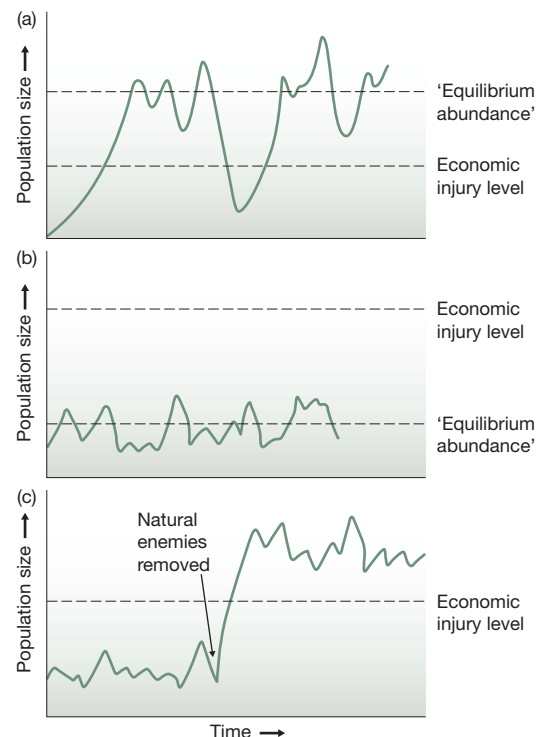
### 12.5.1 Aims of pest control: economic injury levels and action thresholds

EILs for pests, non-pests and potential pests

Economics and sustainability are intimately tied together. Market forces ensure that uneconomic practices are not sustainable. One might imagine that the aim of pest control is total eradication of the pest, but this is not the general rule. Rather, the aim is to reduce the pest population to a level at which it does not pay to achieve yet more control (the *economic injury level* or EIL). The EIL for a hypothetical pest is illustrated in Figure 12.15a. It is greater than zero (eradication is not profitable) but it is also below the typical, average abundance of the species. If the species was naturally self-limited to a density below the EIL, then it would never make economic sense to apply 'control' measures, and the species could

**Figure 12.15**

(a) The population fluctuations of a hypothetical pest. Abundance fluctuates around an 'equilibrium abundance' set by the pest's interactions with its food, predators, etc. It makes economic sense to control the pest when its abundance exceeds the economic injury level (EIL). Being a pest, its abundance exceeds the EIL most of the time (assuming it is not being controlled). (b) By contrast, a species that cannot be a pest always fluctuates below its EIL. (c) 'Potential' pests fluctuate normally below their EIL but rise above it in the absence of one or more of their natural enemies.



not, by definition, be considered a ‘pest’ (Figure 12.15b). There are other species, though, which have a carrying capacity (see Chapter 5) in excess of their EIL, but have a typical abundance that is kept below the EIL by natural enemies (Figure 12.15c). These are potential pests. They can become actual pests if their enemies are removed.

When a pest population has reached a density at which it is causing economic injury, however, it is generally too late to start controlling it. More important, then, is the *economic threshold* (ET): the density of the pest at which action should be taken to prevent it reaching the EIL. ETs are predictions based on detailed studies of past outbreaks or sometimes on correlations with climatic records. They may take into account the numbers not only of the pest itself but also of its natural enemies. As an example, in order to control the spotted alfalfa aphid (*Therioaphis trifolii*) on hay alfalfa in California, control measures have to be taken at specific times under certain circumstances:

- 1 In spring when the aphid population reaches 40 aphids per stem.
- 2 In summer and fall when the population reaches 20 aphids per stem, but the first three cuttings of hay are not treated if the ratio of ladybirds (beetle predators of the aphids) to aphids is one adult per 5–10 aphids, or three larvae per 40 aphids on standing hay, or one larva per 50 aphids on stubble.
- 3 During winter when there are 50–70 aphids per stem (Flint & van den Bosch, 1981).

### 12.5.2 Problems with chemical pesticides, and their virtues

A pesticide gets a bad name if, as is usually the case, it kills more species than just the one at which it is aimed. It may then become a pollutant (see Chapter 13). However, in the context of the sustainability of agriculture, the bad name is especially justified if it kills the pest’s natural enemies and so contributes to undoing what it was employed to do. Thus, the numbers of a pest sometimes increase rapidly some time after the application of a pesticide. This is known as *target pest resurgence* and occurs when treatment kills both large numbers of the pest and large numbers of their natural enemies. Pest individuals that survive the pesticide or that migrate into the area later find themselves with a plentiful food resource but few, if any, natural enemies. The abundance of the pest population may then explode.

target pest resurgence and  
secondary pest outbreaks

The after effects of applying a pesticide may involve even more subtle reactions. When a pesticide is applied, it may not be only the target pest that resurges. Alongside the target are likely to be a number of potential pest species that had been kept in check by their natural enemies (Figure 12.15c). If the pesticide destroys these, the potential pests become real ones – and are called *secondary pests*. A dramatic example concerns the insect pests of cotton in Central America. In 1950, when mass dissemination of organic insecticides began, there were two primary pests: the Alabama leafworm and the boll weevil (Smith, 1998). Organochlorine and organophosphate insecticides were applied fewer than five times a year and initially had apparently miraculous results – crop yields soared. By 1955, however, three secondary pests had emerged: the cotton bollworm, the cotton aphid and the false pink bollworm. The pesticide applications rose

evolved resistance . . .

to 8–10 per year. This reduced the problem of the aphid and the false pink bollworm, but led to the emergence of five further secondary pests. By the 1960s, the original two pest species had become eight and there were, on average, 28 applications of insecticide per year. Clearly, such a rate of pesticide application is not sustainable.

Chemical pesticides lose their role in sustainable agriculture if the pests evolve resistance. The evolution of pesticide resistance is simply natural selection in action (see Chapter 2). It is almost certain to occur when vast numbers of a genetically variable population are killed. One or a few individuals may be unusually resistant (perhaps because they possess an enzyme that can detoxify the pesticide). If the pesticide is applied repeatedly, each successive generation of the pest will contain a larger proportion of resistant individuals. Pests typically have a high intrinsic rate of reproduction, and so a few individuals in one generation may give rise to hundreds or thousands in the next, and resistance spreads very rapidly in a population.

This problem was often ignored in the past, even though the first case of DDT (dichlorodiphenyltrichloroethane) resistance was reported as early as 1946 (houseflies in Sweden). The current scale of the problem is illustrated in Figure 12.16, which shows the exponential increase in the numbers of invertebrates that have evolved resistance and in the number of pesticides against which resistance has evolved. Resistance has been recorded in every family of arthropod pest (including dipterans such as mosquitoes and houseflies, as well as beetles, moths, wasps, fleas, lice, moths and mites) as well as in weeds and plant pathogens. Take the Alabama leafworm (see above), a moth pest of cotton, as an example. It has developed resistance in one or more regions of the world to aldrin, DDT, dieldrin, endrin, lindane and toxaphene.

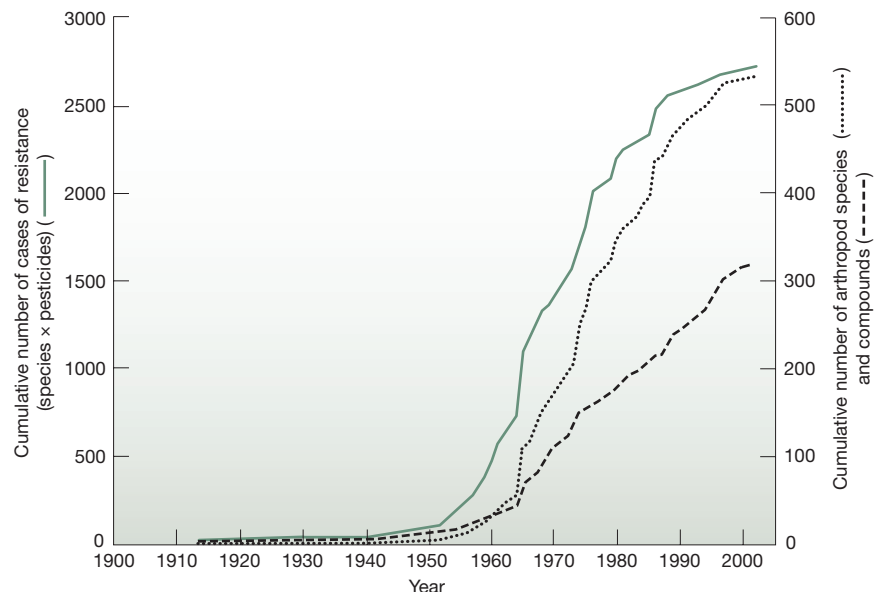
. . . but pesticides work

If chemical pesticides brought nothing but problems, however – if their use was intrinsically and acutely unsustainable – then they would already have fallen out of widespread use. This has not happened. Instead, their rate of production

**Figure 12.16**

Global increases in the number of arthropod pest species reported to have evolved pesticide resistance and in the number of pesticide compounds against which resistance has developed. Each pest, on average, has evolved resistance to more than one pesticide, so there are now more than 2500 cases of evolution of resistance (pests  $\times$  compounds).

FROM MICHIGAN STATE UNIVERSITY'S DATABASE OF ARTHROPODS RESISTANT TO PESTICIDES, WWW.PESTICIDERESISTANCE.ORG/DB/; © PATRICK BILLS, DAVID MOTA-SANCHEZ & MARK WHALON



has increased rapidly. The ratio of cost to benefit for the individual producer has remained in favor of pesticide use: they do what is asked of them. In the USA, insecticides have been estimated to benefit the agricultural producer to the tune of around \$5 for every \$1 spent (Pimentel et al., 1978).

Moreover, in many poorer countries, the prospect of imminent mass starvation, or of an epidemic disease, are so frightening that the social and health costs of using pesticides have to be ignored. In general the use of pesticides is justified by objective measures such as ‘lives saved’, ‘economic efficiency of food production’ and ‘total food produced’. In these very fundamental senses, their use may be described as sustainable. In practice, sustainability depends on continually developing new pesticides that keep at least one step ahead of the pests – pesticides that are less persistent, biodegradable and more accurately targeted at the pests.

### 12.5.3 Biological control

Outbreaks of pests occur repeatedly and so does the need to apply pesticides. But biologists can sometimes replace chemicals by other tools that do the same job and cost a great deal less. Biological control involves the manipulation of the natural enemies of the pests. There are three main types of biological control: importation, conservation and inoculation biological control.

The first is the *importation* of a natural enemy from another geographic area – often the area where the pest originated. The objective is for the control agent to persist and thus maintain the pest below its economic threshold for the foreseeable future. This is a case of a desirable invasion of an exotic species and is often called *classical biological control*.

The most classic example of ‘classical’ biological control concerns the cottony cushion scale insect (*Icerya purchasi*), discovered as a pest of Californian citrus orchards in 1868. By 1886 it had brought the citrus industry to its knees. Species that colonize a new area may become pests because they have escaped the control of their natural enemies. Importation of some of these natural enemies is then, in essence, restoration of the status quo. A search for natural enemies led to the importation to California of two candidate species. The first was a parasitoid, a two-winged fly (*Cryptochaetum* sp.) that laid its eggs on the scale insect, giving rise to a larva that consumed the pest. The other was a predatory ladybird beetle (*Rodolia cardinalis*). Initially, the parasitoids seemed to have disappeared, but the predatory beetles underwent such a population explosion that, amazingly, all scale insect infestations in California were controlled by the end of 1890. Although the beetles have usually taken the credit, the long-term outcome has been that the beetles keep the scale insects in check inland, but *Cryptochaetum* is the main control near the coast (Flint & van den Bosch, 1981). The economic return on investment in biological control was very high in California and the ladybird beetles have subsequently been transferred to 50 other countries.

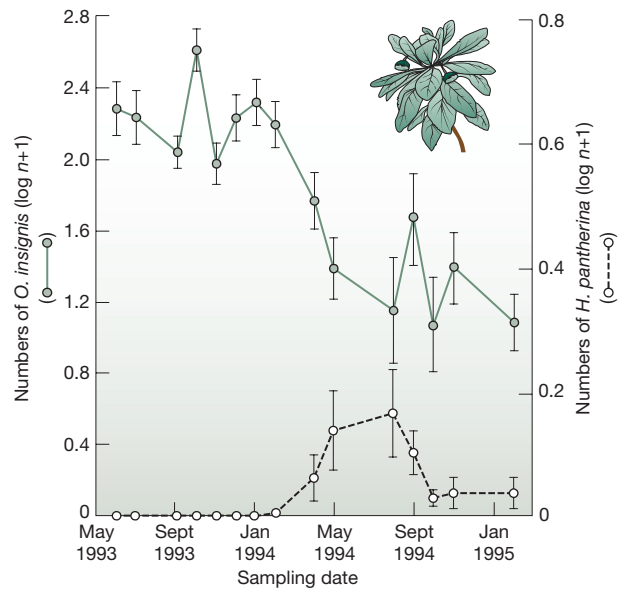
Another invasive scale insect was driving to extinction the national tree of the small South Atlantic island of St. Helena (the last home of another famous invader – Napoleon Bonaparte). Only 2500 St. Helena gumwoods (*Commidendrum robustum*) remained in 1991 as a result of attack by the South American scale insect *Orthezia insignis*. Fowler (2004) estimated that all remaining individuals of

three types of biological control

importation biological control

**Figure 12.17**

Mean numbers ( $\pm$  SE, log scale), on continuously monitored 20 cm branchlets of 30 randomly selected gumwood trees, of the pest scale insect *Orthezia insignis* and its biological control agent, the ladybird *Hyperaspis pantherina*. Mean scale insect numbers dropped from more than 400 adults and nymphs (in September 1993) to fewer than 15 (in February 1995) when sampling ceased. Mean ladybird numbers increased from January to August 1994, coinciding with an obvious decline in scale insects, before ladybird numbers declined again. The highest recorded numbers of ladybirds were 1.3 adults and 3.4 larvae per 20 cm branchlet.



AFTER FOWLER 2004

this rare tree would have been dead by 1995. Another ladybird beetle saved the day. *Hyperaspis pantherina* was cultured and released on St. Helena in 1993 and as its numbers increased there was a corresponding 30-fold decrease in scale insect numbers (Figure 12.17). No scale outbreaks have been reported since 1995 and release of the ladybirds has been discontinued because the ladybird population is maintaining itself at low density in the wild, as good importation biocontrol agents should.

conservation biological control

In contrast to importation biological control, *conservation biological control* involves manipulations to increase the equilibrium density of natural enemies that are already native to the region where the pest occurs. In the case of the aphid pests of wheat (e.g. *Sitobion avenae*), predators that specialize on aphids include ladybirds and other beetles, heteropteran bugs, lacewings (Chrysopidae), fly larvae (Syrphidae) and spiders. Many of these natural enemies spend the winter in grassy boundaries at the edge of wheat fields, from where they disperse to reduce aphid populations around field edges. Farmers can protect grass habitat around their fields and even plant grassy strips in the interior to enhance these natural populations and the scale of their impact on the pests.

control by inoculation

A third class of biological control, *inoculation biological control* is widely practiced in the biological control of pests in glasshouses, where crops are removed, along with the pests and their natural enemies, at the end of the growing season. Two particularly important natural enemies used for inoculation are *Phytoseiulus persimilis*, a mite that preys on the spider mite *Tetranychus urticae*, a pest of roses, cucumbers and other vegetables, and *Encarsia formosa*, a chalcid parasitoid wasp of the whitefly *Trialeurodes vaporariorum*, a pest in particular of tomatoes and cucumbers.

biological control: excellent  
when it works . . .

Insects have been the main agents of biological control against both insect pests and weeds. Table 12.1 summarizes the extent to which they have been used and the proportion of cases where the establishment of an agent has greatly reduced or eliminated the need for other control measures.



Table 12.1

The record of insects as biological control agents against insect pests and weeds.

	INSECT PESTS	WEEDS
Control agent species	563	126
Pest species	292	70
Countries	168	55
Cases where agent has become established	1063	367
Substantial successes	421	113
Successes as a percentage of establishments	40	31

Biological control may appear to be a particularly environmentally friendly approach to pest control, but examples have come to light where even carefully chosen, and apparently successful, introductions of biological control agents have impacted on non-target species (Pearson & Callaway, 2003). *Cactoblastis* moths, which were introduced to Australia and were dramatically successful at controlling exotic cactuses, were accidentally introduced to Florida where they have been attacking several native cacti (Cory & Myers, 2000). Similarly, a seed-feeding weevil (*Rhinocyllus conicus*), introduced to North America to control exotic *Carduus* thistles, attacks several native thistles and has adverse impacts on populations of a native picture-winged fly (*Paracantha culta*) that feeds on the thistle seeds (Louda et al., 1997). Such ecological effects need to be better evaluated in future assessments of potential biocontrol agents.

... but sometimes non-target organisms are affected

## 12.6 Integrated farming systems

The desire for sustainable agriculture has increasingly led to more ecological approaches to food production, which are often given the label ‘integrated farming systems’. Part of this, and something that preceded it historically, is a similar approach to pest control: *integrated pest management* (IPM).

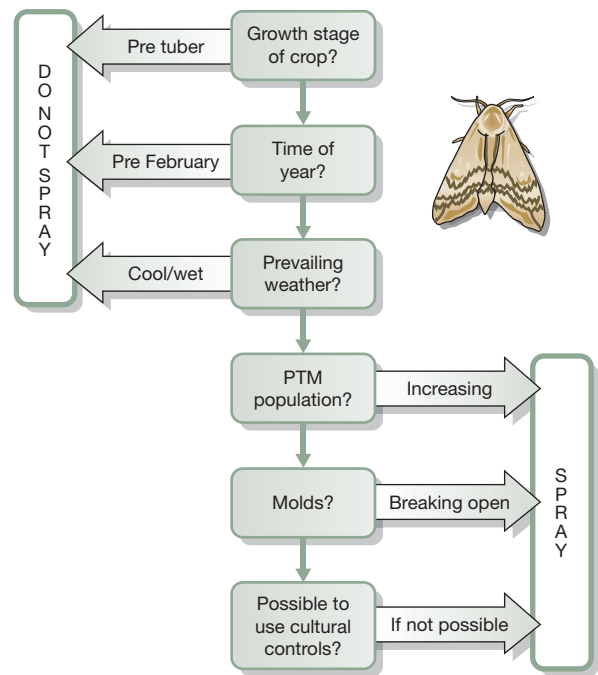
IPM is a practical philosophy of pest management. It combines physical control (for example, simply keeping pests away from crops), cultural control (for example, rotating the crops planted in a field so pests cannot build up their numbers over several years), biological and chemical control and the use of resistant crop varieties. It has come of age as part of the reaction against the unthinking use of chemical pesticides in the 1940s and 1950s.

IPM is ecologically based but uses all methods of control – including chemicals, where appropriate. It relies heavily on natural mortality factors, such as natural enemies and weather, and seeks to disrupt them as little as possible. It aims to control pests below an economically damaging level (the EIL), and it depends on monitoring the abundance of pests and their natural enemies and using various control methods as complementary parts of an overall program. IPM therefore calls for specialist pest managers or advisers. Broad-spectrum pesticides in particular, although not excluded, are used only very sparingly, and if chemicals are used at all it is in ways that minimize the costs and quantities used. The essence of the IPM approach is to make the control measures fit the pest problem, and no two pest problems are the same – even in adjacent fields.

integrated pest management

**Figure 12.18**

Decision flow chart for the integrated pest management of potato tuber moths (PTM) in New Zealand. Boxed phrases are questions (e.g. 'Growth stage of crop?'), words in arrows are the farmer's answers to the questions (e.g. 'Pre tuber') and the recommended action is shown in the vertical boxes (e.g. 'Do not spray'). Note that February is late summer in New Zealand.



AFTER HERMAN, 2000

#### IPM for the potato tuber moth

The caterpillar of the potato tuber moth (*Phthorimaea operculella*) commonly damages crops in New Zealand. An invader from a warm temperate subtropical country, it is most devastating when conditions are warm and dry (i.e. when the environment coincides closely with its optimal niche requirements). There can be as many as 6–8 generations per year and different generations mine leaves, stems and tubers. The caterpillars are protected both from natural enemies (parasitoids) and insecticides when in the tuber, so control must be applied to leaf-mining generations. The IPM strategy for the potato tuber moth (Herman, 2000) involves monitoring (female pheromone traps, set weekly from midsummer, are used to attract males, which are counted), cultural methods (the soil is cultivated to prevent soil cracking, soil ridges are molded up more than once and soil moisture is maintained), and the use of insecticides, but only when absolutely necessary (most commonly the organophosphate, methamidophos). Farmers follow the decision tree shown in Figure 12.18.

#### integrated farming systems: LISA, IFS and LIFE

It has increasingly become apparent, in an agricultural context at least, that implicit in the philosophy of IPM is the idea that pest control cannot be isolated from other aspects of food production and is especially bound up with the means by which soil fertility is maintained and improved. Thus, a number of programs have been initiated to develop and put into practice sustainable food production methods that incorporate IPM, including not only IFS (integrated farming systems) but also LISA (low input sustainable agriculture) in the USA and LIFE (lower input farming and environment) in Europe (International Organisation for Biological Control, 1989; National Research Council, 1990). All share a commitment to the development of sustainable agricultural systems.

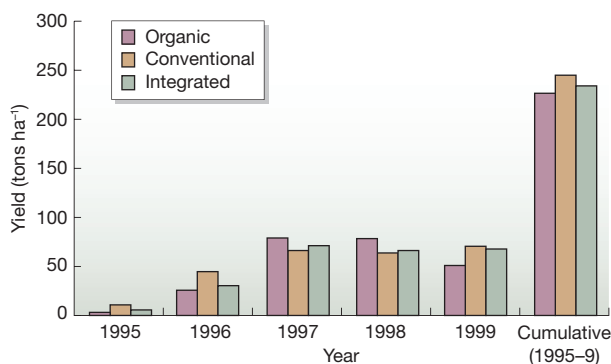


Figure 12.19

Fruit yields (metric tons per hectare) of three apple production systems.

These approaches have advantages in terms of reduced environmental hazard. Even so, it is unreasonable to suppose that they will be adopted widely unless they are also sound in economic terms. As we have already noted, in an industry such as agriculture, practices that are economically unsustainable are, ultimately, unsustainable overall. In this context, Figure 12.19 shows the yields of apples from organic, conventional and integrated production systems in Washington State from 1994 to 1999 (Reganold et al., 2001). Organic management excludes such conventional inputs as synthetic pesticides and fertilizers whilst integrated farming uses reduced amounts of chemicals by integrating organic and conventional approaches. All three systems gave similar apple yields but the organic and integrated systems had higher soil quality and potentially lower environmental impacts. When compared with conventional and integrated systems, the organic system produced sweeter apples, higher profitability and greater energy efficiency.

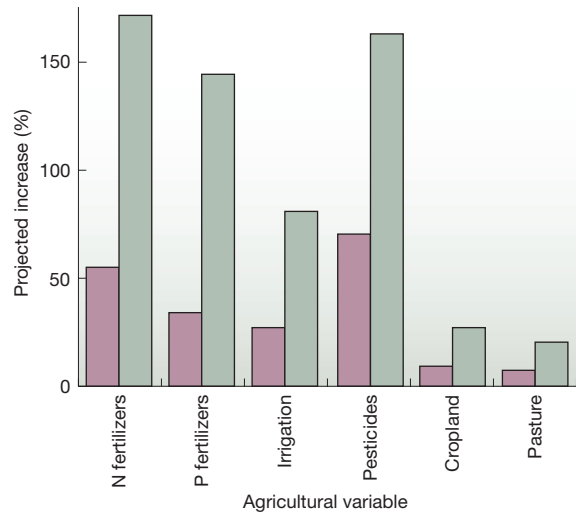
environmental and economic sustainability

## 12.7 Forecasting agriculturally driven global environmental change

Much attention has been focused on the predicted far-reaching consequences of global climate change caused by human activities such as the burning of fossil fuels. We deal with this in Chapter 13. However, very significant threats are also posed to ecosystems around the world by increasing agricultural development. In this chapter we have considered the problems of the more-than-exponential increase in the human population, and of the associated impacts of increased erosion, unsustainability of water supply, salinization and desertification, excess plant nutrients finding their way into waterways, and unwanted consequences of chemical pesticides. Model projections suggest that all these will increase over the next 50 years as more land is converted to grow crops and pasture (Tilman et al., 2001) (Figure 12.20). This can be expected to place biodiversity at high risk, particularly because population increases are predicted to be greatest in species-rich tropical areas. To control the environmental impacts of agricultural expansion, we will need scientific and technological advances as well as the implementation of effective government policies.

**Figure 12.20**

Projected increases in nitrogen (N) and phosphorus (P) fertilizers, irrigated land, pesticide use and total areas under crops and pasture by the years 2020 (maroon bars) and 2050 (green bars).



FROM LAURANCE 2001, BASED ON DATA IN TILMAN ET AL., 2001



## Summary

### The human population 'problem'

Resource use by humans is defined as sustainable if it can be continued for the foreseeable future. The root of most environmental problems is the 'population problem': a large human population that has been growing at a more-than-exponential rate.

Three groups of nations can be recognized: those that passed through the demographic transition 'early', 'late' or 'not yet'. Even if it were possible instantaneously to bring about the transition in all remaining countries of the world, the population problem would not be solved, partly because population growth has its own momentum.

The global carrying capacity for humans is variously estimated at between 1 and 1000 billion, depending mainly on what is deemed to constitute an acceptable standard of living.

### Harvesting living resources from the wild

Whenever a natural population is exploited by harvesting there is a risk of overexploitation. But harvesters also want to avoid underexploitation – when potential

consumers are deprived of resources and those who do the harvesting are underemployed.

The concept of the maximum sustainable yield (MSY) has been a guiding principle in the exploitation of natural populations. There are two simple ways of obtaining an MSY on a regular basis: through a 'fixed quota' and through a 'fixed effort'. Two limitations of the MSY approach are: (i) that it treats all individuals in the population as identical; and (ii) that it treats the environment as unvarying. Improved harvesting strategies correct both these oversights. Lack of knowledge of most fisheries around the world means that management is often based on the precautionary principle, often in the absence of data.

### The farming of monocultures

Increasingly, animals and plants have been domesticated and managed in ways that allowed much larger harvests – usually as monocultures. But a high price may be paid to maintain these high rates of food production. Monocultures offer ideal conditions for the

epidemic spread of diseases and lead to widespread degradation of land.

### The sustainability of soil and of water supplies

In an ideal sustainable world, new soil would be formed as fast as the old was lost, but in most agricultural systems this is not achieved. When there is an overwhelming reliance on artificial fertilizers, maintaining the organic matter capital of the soil tends to be neglected and this has declined worldwide.

Soil degradation can be slowed down by incorporating manures and residues, alternating cultivation and fallow periods, or returning the land to grazed pasture. In tropical regions, terracing is widely practiced over hilly and mountainous terrain. In arid regions, overgrazing and excessive cultivation can lead to desertization and salinization.

Water is widely thought to be the resource that future wars will be fought over. On a global scale, agriculture is the largest consumer of fresh water. Pumping water from underground aquifers is the main cause of loss of agricultural land through salinization.

### Pest control

The aim of pest control is to reduce the pest population to its economic injury level (EIL), but a so-called economic threshold may be of more immediate importance.

Pesticides may kill species other than their target and may give rise to target pest resurgence or

secondary pest outbreaks. Pests may also evolve pesticide resistance.

Biologists may also manipulate the natural enemies of pests (biological control) via three forms of biological control – importation, conservation or inoculation – but even biocontrol agents can have unwanted effects on non-target species.

### Integrated farming systems

Integrated pest management (IPM) is a practical philosophy of pest management that is ecologically based but uses all methods of control where appropriate. It relies heavily on natural mortality factors and calls for specialist pest managers or advisers.

Implicit in the philosophy of IPM is the idea that pest control cannot be isolated from other aspects of food production. A number of programs have been initiated to develop and put into practice sustainable food production methods that incorporate IPM. Evidence has been accumulating that this sustainable farming approach can yield improved economic returns too.

### Agriculturally induced global change

It is clear that very significant threats are posed to ecosystems around the world by the increasing human population and concomitant increases to agricultural development. These are expected to have a particularly damaging effect on biodiversity because most agricultural growth is predicted to occur in the species-rich tropics.

## Review questions

### REVIEW QUESTIONS

Asterisks indicate challenge questions

- 1\* What is sustainability? Is it possible to have sustainable population growth? Sustainable use of fossil fuels? Sustainable use of forest trees? Justify your answers.
- 2 Describe what is meant by 'the demographic transition' in a human population. Explain why it might be important, for future management of human population growth, to discover whether the demographic transition is an academic ideal or a process through which all human populations necessarily pass.

- 3\* The number of people that the Earth can support depends on their standard of living. Argue the case either for or against developing nations having the right to expect standards of living those in the developed world take for granted.
- 4 Contrast the ways in which 'fixed quota' and 'fixed effort' harvesting strategies seek to extract maximum sustainable yields from natural populations.
- 5 Discuss the pros and cons of agricultural monocultures.
- 6 One of the main bodies regulating the production of organic food (food produced without synthetic fertilizers or pesticides) in the United Kingdom is the Soil Association. Explain why you think it has adopted this name.
- 7 Explain the meaning and importance of the terms economic injury level and economic threshold.
- 8 Weigh up the advantages and disadvantages of the chemical and biological control of pests.
- 9 Explain why methods of pest control and methods of soil fertility maintenance need to be considered together in integrated farming systems.
- 10\* Hilborn and Walters (1992) have suggested that there are three attitudes that ecologists can take when they enter the public arena. The first is to claim that ecological interactions are too complex, and our understanding and our data too poor, for definite pronouncements to be made (for fear of being wrong). The second possibility is for ecologists to concentrate exclusively on ecology and arrive at a recommendation designed to satisfy purely ecological criteria. The third is for ecologists to make ecological recommendations that are as accurate and realistic as possible, but to accept that these will be incorporated with a broader range of factors when management decisions are made – and may be rejected. Which of these do you favor, and why?

# Chapter 13



## Habitat degradation

### *Chapter contents*

#### CHAPTER CONTENTS

- 13.1 Introduction
- 13.2 Degradation via cultivation
- 13.3 Power generation and its diverse effects
- 13.4 Degradation in urban and industrial landscapes
- 13.5 Maintenance and restoration of ecosystem services

### *Key concepts*

#### KEY CONCEPTS

In this chapter you will:

- realize that *Homo sapiens* is just one species among many whose activities can reduce the quality of their environment – but to a dramatically greater extent
- understand that we have both physical effects (such as desertization and changes to riverflow) and chemical impacts (pollution by nitrates, carbon dioxide, chlorofluorocarbon, etc.)
- recognize that most pollutants produced on land ultimately affect the atmosphere or rivers, lakes and oceans
- understand that power generation is responsible for the most far-reaching environmental impacts when the carbon dioxide released contributes to global climate change
- appreciate the value to human welfare of ecosystem services lost when we degrade habitats



*As the human population has grown and new technologies have been developed, we have had an ever-increasing impact on natural ecosystems. Physical degradation and chemical pollution associated with cultivation, power generation, urban life and industry have adversely affected human health and many 'ecosystem services' that were free and contributed greatly to human welfare. Our environmental problems have ecological, economic and sociopolitical dimensions, so a multidisciplinary approach will be needed to find solutions.*

## 13.1 Introduction

### 13.1.1 Physical and chemical impacts of human activities

People destroy or degrade natural ecosystems to make way for agricultural, urban and industrial development. We physically damage the natural world when mining for non-renewable resources such as gold and oil, and even exploitation of a renewable resource can disrupt habitat when, for example, bottom trawling for fish damages deep-sea coral communities. The worldwide scale of damage is even greater as a result of chemical pollution produced by human activities such as defecation, cultivation, power generation and industry.

Humans are not unique in degrading their environment. Feces, urine and dead bodies of animals are sometimes sources of pollution in their immediate environments – cattle avoid grass near their waste for several weeks, many birds carry away the fecal sacs of their nestlings and the 'undertaker' caste of honeybees removes dead bodies from the hive. Like us, many species also make profound physical changes to their habitats. Among the 'ecological engineers' of the natural world are beavers that construct dams, prairie dogs that build underground towns and freshwater crayfish that clear sediment from the riverbed. In each case, other species in the community are affected. And there are even species that, like farmers, increase plant nutrient concentrations in their habitats (leguminous plants – see Section 8.4.6), and others that produce 'pesticides' (certain plants produce allelochemicals, the function of which appears to be the inhibition of growth of neighbors).

When population density was low, and prior to our harnessing of non-food energy, humans probably had no greater impact than many other species. But now the scale of human effects is proportional to our huge numbers and the advanced technologies we employ.

Physical degradation of habitats includes soil loss and desertization caused by intensive agriculture (discussed in Section 12.4.1) and changes to river discharge as a result of water impoundment for hydropower generation or abstraction for irrigation of crops (Section 13.2.5).

Chemical degradation has many causes. Pesticides are applied to land but find their way to places they were not intended to be – passing up food chains

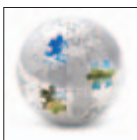
*Homo sapiens* – just another species?

the scale of human degradation reflects our population density and technology

physical degradation of habitats

chemical degradation – pollution

(Box 13.1) and moving via ocean currents to the ends of the Earth. A plethora of other exotic chemicals enter the natural environment from a variety of industrial sources. But the most far-reaching kinds of chemical degradation result not from our production of exotic chemicals but rather the augmentation of simple compounds that already occur naturally. The heavy use on land of nitrogen fertilizer spills into rivers, lakes and oceans, where raised levels of nitrate severely disrupt ecosystem processes – with blooms of microscopic algae shading out waterweeds and, when the algae die and decompose, reducing oxygen and killing animals. Another pollutant route is via the atmosphere. Thus, hundreds of kilometers downwind of large population centers, acid rain (caused by emission of oxides of nitrogen and sulfur from power generation) kills trees and drives lake fish



## 13.1 Topical EConcerns

### Pollution and the thickness of birds' eggshells

The peregrine falcon (*Falco peregrinus*) is a particularly distinctive and beautiful bird of prey with an almost worldwide range. Until the 1940s, about 500 pairs bred regularly in the eastern states of the United States and about 1000 pairs in the west and in Mexico. In the late 1940s their numbers started a rapid decline, and by the mid-1970s the bird had disappeared from almost all the eastern states and its numbers had fallen by 80–90% in the west. Similar dramatic declines were occurring in Europe. Peregrine falcons were listed as an *endangered species* (at risk of extinction). The decline also occurred in many other birds of prey and was traced to failure to hatch normal broods. There was very high breakage of eggs in the nest.

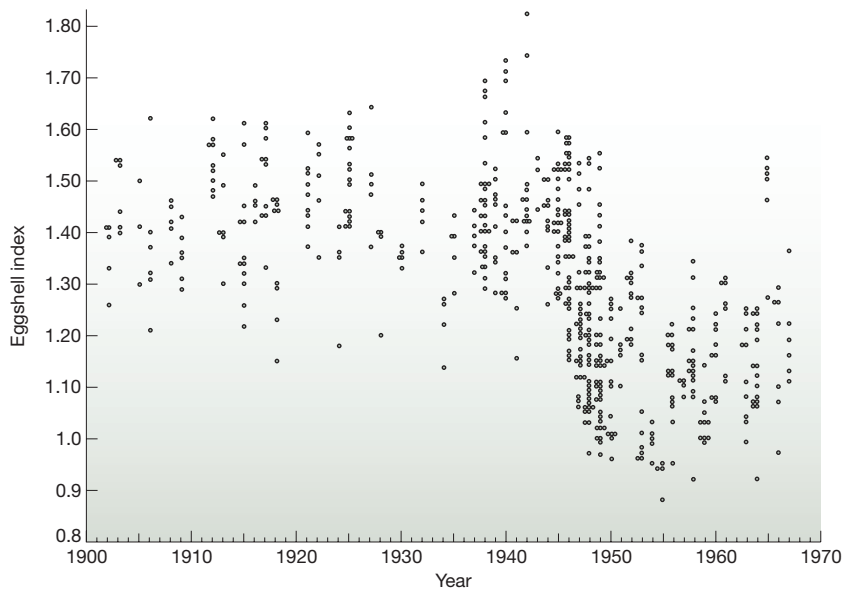


© JEAN HOSKINS, FLPA 02176-00109-147

The cause was eventually identified as the accumulation of DDT (dichlorodiphenyltrichloroethane) in the parent birds. The pesticide had apparently contaminated seeds and insects that had then been eaten by small birds and had accumulated in their tissues. In turn these had been caught and eaten by birds of prey and the pesticide interfered with their reproduction – in particular causing the eggs to have thin shells and be more likely to break.

The use of DDT was banned in the United States in 1972. Programs were developed to breed peregrines in captivity and at least 4000 peregrines were bred and released to the wild. Peregrines are now breeding successfully over much of the United States and are no longer considered an endangered species. In Britain, recovery has been so successful that the peregrine has become regarded as a pest by pigeon fanciers and lovers of the smaller songbirds.

It was possible to identify DDT pollution as a cause of eggshell thinning because eggshells had been collected as dated specimens in museums and private collections. A measure of eggshell thickness in collections of eggs of the sparrow hawk (*Accipiter nisus*) showed a sudden stepwise fall of 17% in 1947, when DDT began to be used widely in agriculture, and a steady increase in thickness after DDT was banned (Figure 13.1).



**Figure 13.1**

Graph showing the changes in sparrowhawk eggshell thickness (museum specimens) in Britain.

FROM RATCLIFFE, 1970

It was a surprise to ornithologists in Britain to find evidence of a decline in eggshell thickness of 2–10% in four species of thrush (*Turdus*) since the mid-19th century (Green, 1998). This seemed to have started long before the development of organic pesticides and there was no sudden change when DDT was introduced. Snails are an important part of the diet of thrushes; thrushes derive much of the calcium for their eggshells from snails. There is convincing evidence

that acid rain, caused by release to the atmosphere of sulfur and nitrogen oxides from power generation and industry, has acidified leaf litter and reduced its calcium content, leading to a reduction in snail populations and in the calcium content of their shells. The shells of wild birds' eggs have therefore recorded two of the major, but quite different, forces of environmental pollution: pesticides (Section 13.2.5) and acid rain (Section 13.3.1).

extinct. And the biggest pollution problem of all involves the augmentation, via the burning of fossil fuels, of carbon dioxide in the atmosphere. The consequent global climate change has implications for every ecosystem in the world.

Our discussion of human degradation of habitats will first consider the consequences of cultivation (Section 13.2), before proceeding to an assessment of damage associated with the generation of power (Section 13.3), and then the ecological consequences of life in urban and industrial landscapes (Section 13.4). But first (Section 13.1.2) we will note how the cost of our activities can be tallied in relation to the free 'ecosystem services' that are lost when habitats are degraded. Discussion returns to this theme in the final section (13.5), which strikes a more optimistic note by discussing actions that can be taken to maintain or restore ecosystem services.



Acid rain damage to spruce forest.

© ROB AND ANNI SIMPSON, VISUALS UNLIMITED

### 13.1.2 Economic costs of human impacts: lost ecosystem services

Biodiversity has intrinsic value. But there is also a utilitarian view of nature that focuses on the services that ecosystems provide for people to use and enjoy. *Provisioning services* include wild foods such as fish from the ocean and berries from the forest, medicinal herbs, fiber, fuel and drinking water, as well as the products of cultivation in agroecosystems. Nature also contributes the *cultural services* of esthetic fulfilment and educational and recreational opportunities. *Regulating services* include the ecosystem's ability to break down or filter out pollutants, the moderation by forests and wetlands of disturbances such as floods, and the ecosystem's ability to regulate climate (via the capture or 'sequestration' by plants of the greenhouse gas carbon dioxide). Finally, and underlying all the others, there are *supporting services* such as primary production, the nutrient cycling upon which productivity is based, and soil formation.

In the case of three important provisioning services – production of crops, livestock and aquaculture – human activities have had a positive effect. And because of increased tree planting in some parts of the world there has even been a global improvement in the sequestration of carbon by trees (a climate regulating service).

But we have degraded most of the other services (Millennium Ecosystem Assessment 2005). As discussed in Chapter 12, many fisheries are now overexploited (a negative effect on this provisioning service), while intensive agriculture has worked against the ecosystem's ability to replace soil lost to erosion (a regulating service). The continuing loss of forest in tropical regions has negative effects on the ability of the terrestrial ecosystem to regulate riverflow – deforestation increases flow during flooding and decreases it during dry periods. And, as we saw in Section 1.3.3, deforestation (or even just the loss of riverside vegetation) can diminish the terrestrial ecosystem's capacity to hold and recycle nutrients (another regulating service), releasing large quantities of nitrate and other plant nutrients

provisioning, cultural, regulating  
and supporting services

a few positive human effects on  
ecosystem services . . .

. . . but many negative effects

a valuation of ecosystem  
services . . .

into waterways. Note that the modification of an ecosystem to enhance one service (e.g. intensification of agriculture to produce more crop per hectare – a provisioning service) generally comes at a cost to other services previously provided (loss of regulating services such as nutrient uptake and of cultural services such as sacred sites, streamside walks and valued biodiversity) (Townsend, 2007).

The concept of ecosystem services is important because it focuses on how ecosystems contribute to human well-being, providing a counterpoint to the economic reasons that justify our degradation of nature in the first place (to produce food, fiber, fuel, housing and luxury products for a burgeoning human population).

Economists can put a value on nature in a variety of ways. A provisioning service for which there is a market is straightforward – values are easily ascribed to clean water for drinking or irrigation, to fish from the ocean and medicinal products from the forest. A more imaginative approach is required in other situations. Thus, the *travel cost* that tourists are willing to pay to visit a natural area provides a minimum value of the cultural service provided. To determine *contingent valuation*, surveys of the public assess their willingness to pay for each of a set of alternative land use scenarios; the answer is thus ‘contingent’ on a specific hypothetical scenario and description of the environmental service concerned. *Replacement cost* estimates how much would need to be spent to replace an ecosystem service with a man-made alternative, for example by substituting the natural waste disposal capacity of a wetland by building a treatment works. And when an ecosystem service has already been lost, the real costs become apparent. Take, for example, the largely deliberate burning of 50,000 km<sup>2</sup> of Indonesian vegetation in 1997 – the economic cost comprised US\$4.5 billion in lost forest products and agriculture, increased greenhouse gas emissions, reductions to tourism and healthcare expenditure on 12 million people affected by the smoke (Balmford & Bond 2005).

. . . adding up to a global total of  
\$38 trillion

Costanza et al. (1997) added up all ecosystem services worldwide, arriving at an estimate of US\$38 trillion (10<sup>12</sup>) – more than the gross domestic product of all nations combined. This ‘new economics’ provides persuasive reasons for taking greater care of ecosystems and the biodiversity they contain.

## 13.2 Degradation via cultivation

When intensive livestock production forces animals to live the equivalent of urban life, their waste is produced faster than natural decomposers and detritivores can handle it (see Chapter 11). All the problems of human urban overpopulation then apply to domestic livestock. Intensive agriculture is also associated with an increase in the level of the nitrate and phosphate that runs into rivers and lakes (and into drinking water) and problems associated with the use of insecticides and herbicides. As we have already seen in Section 12.7, the environmental threats posed by agricultural intensification are expected to increase in the coming decades.

### 13.2.1 Intensive livestock management

excreta from cattle and pigs is  
bulky (and smelly) but poultry  
waste is more acceptable

Pigs, cattle and poultry are the three major contributors to pollution in industrialized agriculture feedlots. The waste from factory-farmed poultry is easily dried and forms a transportable, inoffensive and valuable crop and garden fertilizer. In contrast, the excreta from cattle and pigs are 90% water and have an unpleasant

smell. A commercial unit for fattening 10,000 pigs produces as much pollution as a town of 18,000 inhabitants.

The law in many parts of the world increasingly restricts the discharge of agricultural slurry into watercourses. The simplest and often the most economically sound practice returns the material to the land as semisolid manure or as sprayed slurry. This dilutes its concentration in the environment to what might have occurred in a more primitive and sustainable type of agriculture and converts pollutant into fertilizer. Soil microorganisms decompose the organic components of sewage and slurry and most of the mineral nutrients become immobilized in the soil, available to be absorbed again by the vegetation.

Nitrogen is a special case: nitrate ions are not adsorbed in the soil and rainfall leaches them into drainage (and therefore potential drinking) water. The nitrate becomes a new pollutant and one of the biggest culprits is farm specialization where forage crops are grown in one area, but stock is fattened on the other side of the country. This means that fertilizer must be used to make up the shortfall when plants are reaped and transported to the stock, whose excreta can hardly be shipped all the way back to the farm of origin. In the USA, for example, only 34% of the nitrogen excreted in animal waste is returned to fields where the crops are grown (Mosier et al., 2002). Much of the rest eventually finds its way into streams and rivers. A change in practice to one where animal feed crops and stock fattening occur in the same area would certainly reduce nutrient loss to waterways.

### 13.2.2 Intensive cropping

Some of the nitrogen used in agricultural fertilizer is obtained by mining potassium nitrate in Chile and Peru, and some, as we have seen, comes from animal excreta, but the majority comes from the energy-expensive industrial process of nitrogen fixation, in which nitrogen is catalytically combined with hydrogen under high pressure to form ammonia and, in turn, nitrate. However, it is wrong to regard artificial fertilization as the only practice that leads to nitrate pollution; nitrogen fixed by crops of legumes such as alfalfa, clover, peas and beans also finds its way into nitrates that leach into drainage water.

Excess nitrates in drinking water can be a health hazard – the Environmental Protection Agency in the United States recommends a maximum concentration of 10 mg l<sup>-1</sup> in drinking water. Nitrates may contribute to the formation of carcinogenic nitrosamines and, in young children, may reduce the oxygen-carrying capacity of the blood. Public water systems are required to be monitored regularly and violations reported to the federal government. In 1998, for example, nearly 0.2% of children in the USA (117,000 children in all) lived in areas in which the nitrate standard was exceeded.

There are a number of tools to minimize fertilizer loss from the land (thus saving money) to the water (where a useful resource becomes an irritating pollutant). Farmers might aim to maintain a ground cover of vegetation year-round, practice mixed cropping rather than monoculture and take care to return organic matter to the soil. The overriding objective should be to match nutrient supply to crop demand. Modern ‘controlled release’ fertilizers hold much promise in this regard (Mosier et al., 2002).

The excess input of nutrients, both nitrogen- and phosphorus-based, from agricultural runoff (and human sewage) has caused many ‘healthy’ *oligotrophic* lakes

most agricultural crops depend on fertilizer nitrogen – or nitrogen fixation by legumes

nitrates in drinking water are a hazard to health

tools to minimize fertilizer loss from land



downstream problems of  
fertilizer runoff

cultural eutrophication of lakes  
and oceans

reversing cultural eutrophication  
of lakes – ‘bottom up’ by  
chemical means . . .

. . . or top down by  
biomanipulation

constructing wetlands to manage  
ocean water quality

(low nutrient concentrations, low plant productivity with abundant water weeds, and clear water) to switch to a *eutrophic* condition where high nutrient inputs lead to high phytoplankton productivity (sometimes dominated by bloom-forming toxic species). This makes the water turbid, eliminates large plants and, in the worst situations, leads to anoxia and fish kills: so-called *cultural eutrophication*. Thus, important ecosystem services are lost, including the provisioning service of wild-caught fish and the cultural services associated with recreation.

The process of *cultural eutrophication* of lakes has been understood for some time. But only recently did scientists notice huge ‘dead zones’ in the oceans near river outlets, particularly those draining large catchment areas such as the Mississippi in North America and the Yangtze in China. The nutrient-enriched water flows through streams, rivers and lakes, and eventually to the estuary and ocean where the ecological impact may be huge, killing virtually all invertebrates and fish in areas up to 70,000 km<sup>2</sup> in extent. More than 150 sea areas worldwide are now regularly starved of oxygen as a result of decomposition of algal blooms, fueled particularly by nitrogen from agricultural runoff of fertilizers and sewage from large cities (UNEP, 2003). Oceanic dead zones are typically associated with industrialized nations and usually lie off countries that subsidize their agriculture, encouraging farmers to increase productivity and use more fertilizer.

### 13.2.3 Managing eutrophication

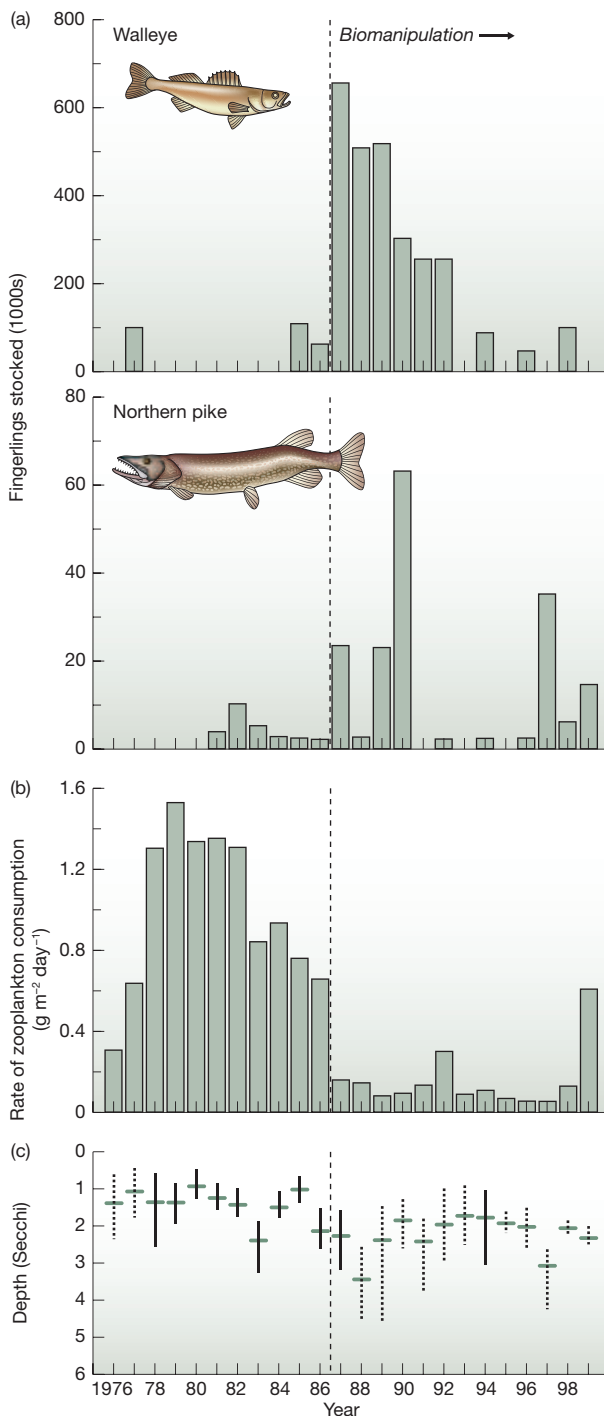
Lake eutrophication, where phosphorus is often the principal culprit, can be reversed by either chemical or biological means. Reduction of phosphorus inputs, by better managing fertilizer use, may be combined with an intervention such as chemical treatment to immobilize phosphorus in the sediment; recovery to a more oligotrophic state can occur within 10–15 years (Jeppesen et al., 2005). In essence, this is *bottom-up control* (see Section 9.5.1) of nutrient availability, reducing phytoplankton productivity and increasing water quality.

The aim of biological control – known as *biomanipulation* – is also to reduce phytoplankton density and increase water clarity, but via an increase in grazing by zooplankton resulting from the active reduction of the biomass of zooplanktivorous fish (by fishing them out or by increasing piscivorous fish biomass). The outcome is the same, but the process is now *top-down control* of a cascade in the food web.

Lathrop et al. (2002) biomanipulated Lake Mendota in Wisconsin, USA, by increasing the density of two piscivorous fish: walleye (*Stizostedion vitreum*) and northern pike (*Esox lucius*). More than 2 million fingerlings of the two species were stocked beginning in 1987 (Figure 13.2a) and total piscivore biomass stabilized at 4–6 kg ha<sup>-1</sup>. The biomass of zooplanktivorous fish declined, as a result of increased predation by the piscivores, from 300–600 kg ha<sup>-1</sup> prior to biomanipulation to 20–40 kg ha<sup>-1</sup> in subsequent years. The consequent reduction in predation pressure on zooplankton (Figure 13.2b) led, in turn, to a switch from small zooplankton grazers (*Daphnia galeata mendotae*) to the larger and more efficient *Daphnia pulicaria*. The increased grazing pressure had the desired effect of reducing phytoplankton density and increasing water clarity (Figure 13.2c).

The only way to alleviate problems in the world’s oceans is by careful management of terrestrial catchment areas to reduce agricultural runoff of nutrients and by treating sewage to remove nutrients before discharge (known as tertiary treatment – Section 13.4.1). The vegetation zones between land and water, such



**Figure 13.2**

(a) Fingerlings of two piscivorous fish stocked in Lake Mendota; the major biomanipulation effort started in 1987 (vertical dashed line). (b) Estimates of zooplankton biomass consumed by zooplanktivorous fish per unit area per day. The principal zooplanktivorous fish were *Coregonus artedii*, *Perca flavescens* and *Morone chrysops*. Note that the consumption of zooplankton was reduced because the piscivorous fish reduced densities of the zooplanktivorous fish. (c) Mean and range of the maximum depth at which a Secchi disk is visible (a measure of water clarity) during the summer from 1976 to 1999. The dotted vertical lines are for periods when the large and efficient grazer *Daphnia pulicaria* was dominant. This grazing zooplankton species was much more prominent after biomanipulation had allowed zooplankton to increase in density; *D. pulicaria* plays a large role in reducing the density of phytoplankton so that water clarity increases (Secchi disk visible at greater depth).

as wetland areas (consisting of swamps, ditches and ponds) and riparian forest along the banks of streams, can be particularly beneficial because the plants and microorganisms remove some of the dissolved nutrients as they filter through the soil. In this way, the riparian zone provides a regulating ecosystem service.

### Figure 13.3

The locations of 148 wetlands under construction along tributaries of the Rönneå River in southern Sweden. If these are built to occupy 5% of the total land area, a 40% reduction can be expected in agricultural nitrogen input to the Baltic Sea.



FROM VERHOEVEN ET AL., 2006. BASED ON ARHEIMER & WITTGREN, 2002

But riparian and wetland communities have often been destroyed to provide a greater area for agricultural production. These ecosystems can sometimes be restored to a seminatural state. An alternative is ‘treatment wetlands’, which are constructed, planted and have water flow controlled to maximize the removal of pollutants from the water draining through them. Estimates for catchment areas in southern Sweden, which are a major source of nitrate enrichment of the Baltic Sea, indicate that to remove 40% of the nitrogen currently finding its way into the sea, a system of wetlands covering about 5% of the total land area would need to be recreated (Figure 13.3).

### 13.2.4 Pesticide pollution

Many of the manufactured chemicals that are used to kill pests have become important environmental pollutants. The most widely polluting pesticides are those used to control pests and weeds that damage crops in agriculture, horticulture and forestry or to kill pests that transmit diseases of livestock and humans. All are sprayed or dusted onto the areas in which the pests live, but only a very small proportion hits the target – most lands on the crop or on bare ground. Such pesticides are therefore used in much larger quantities than strictly necessary. The characteristics of the most widely used pesticides were described in Chapter 12.

In the early industrial development of pesticides, manufacturers were not much concerned with the specificity of their product. The potential for disaster is illustrated by the occasion when massive doses of the insecticide dieldrin were applied to large areas of Illinois farmland from 1954 to 1958 to ‘eradicate’ a grassland pest, the Japanese beetle. Cattle and sheep on the farms were poisoned, 90% of the cats on the farms and a number of dogs were killed, and among wildlife 12 species of mammals and 19 species of birds suffered losses (Luckman & Decker, 1960).

Chemical insecticides are generally intended to control particular target pests at particular places and times. Problems arise when they are toxic to many more species than just the target and particularly when they drift beyond the target areas and persist in the environment beyond the target time. The organochlorine insecticides have caused particularly severe problems because they are *biomagnified*. Biomagnification happens when a pesticide is present in an organism that becomes the prey of another and the predator fails to excrete the pesticide. It then accumulates in the body of the predator. The predator may itself be eaten by a further predator, and the insecticide becomes more and more concentrated as it passes up the food chain. Top predators in aquatic and terrestrial food chains, which were never intended as targets, can then accumulate extraordinarily high doses (Figure 13.4; see also Box 13.1).

pesticides are most polluting when they are unselective, persistent and if they 'biomagnify' in food chains

### 13.2.5 Physical degradation associated with cultivation

It hardly needs stating that one of the biggest impacts of cultivation is the physical loss of natural habitats, together with the species they contain. Sometimes, however, the impact is more subtle. A large proportion of the world's crops depend on insect pollinators and bees play a leading role. Farmers often rely on domesticated honeybees (*Apis mellifera*), importing hives when their crops are in flower. However, many wild bee species also pollinate crops (providing a free provisioning ecosystem service) and these species are much less abundant in landscapes that retain little natural vegetation.

loss of natural habitat to cultivation

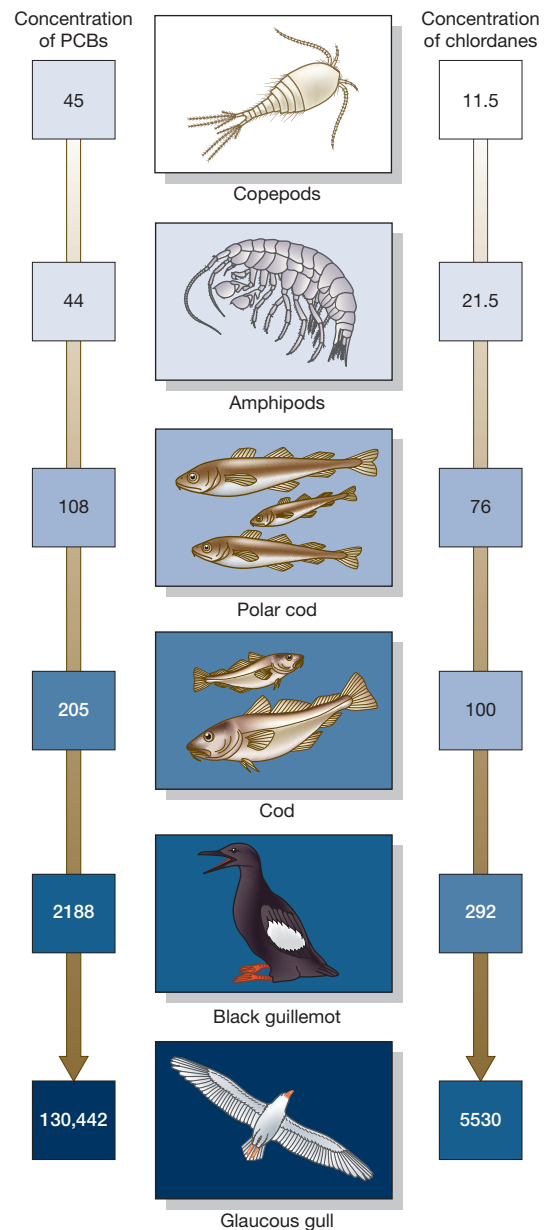
Kremen et al. (2004) studied the role played by native bees in watermelon (*Citrullus lanatus*) fields on Californian farms that varied in the proportion of native and other habitats found nearby. Satellite imagery was used to quantify native upland habitat (woodland and chaparral), riparian woodland and highly modified land classes (agriculture, grassland dominated by non-native species, urban land) in the vicinity of each field. Kremen's team found that the proportion of upland native habitat within 1–2.4 km of the fields was strongly correlated with deposition of watermelon pollen by native bees, reflecting maximum flight distances of about 2.2 km for species that nest in these natural habitats. Next they calculated the proportion of surrounding land that must consist of upland native habitat to yield the 500–1000 pollen grains required per watermelon plant to produce marketable fruit. It turns out that 40% of habitat within 2.4 km of a field needs to be upland native habitat to provide sufficiently for melon pollination needs, providing a strong economic argument to conserve these natural habitats. For farms that are far from natural habitat, active restoration with native plants in hedgerows and ditches and around fields, barns and roads, might allow a target of about 10% native habitat to be achieved (equating to 20–40% of watermelon pollination needs).

Increasing agricultural intensity is usually associated with the removal of surface and ground water for irrigation. Coupled with impoundment of river water behind dams, this abstraction for irrigation can have dramatic physical consequences for patterns in riverflow. Thus, for example, the Nile in Africa, the Yellow River in China and the Colorado River in North America dry up for parts of the year before they reach the ocean. In many less dramatic cases, water abstraction for agricultural, industrial and domestic use changes the hydrographs (discharge patterns) of rivers both by reducing discharge (volume per unit time) and by altering daily and seasonal patterns of flow.

changes to river discharge via impoundment and irrigation

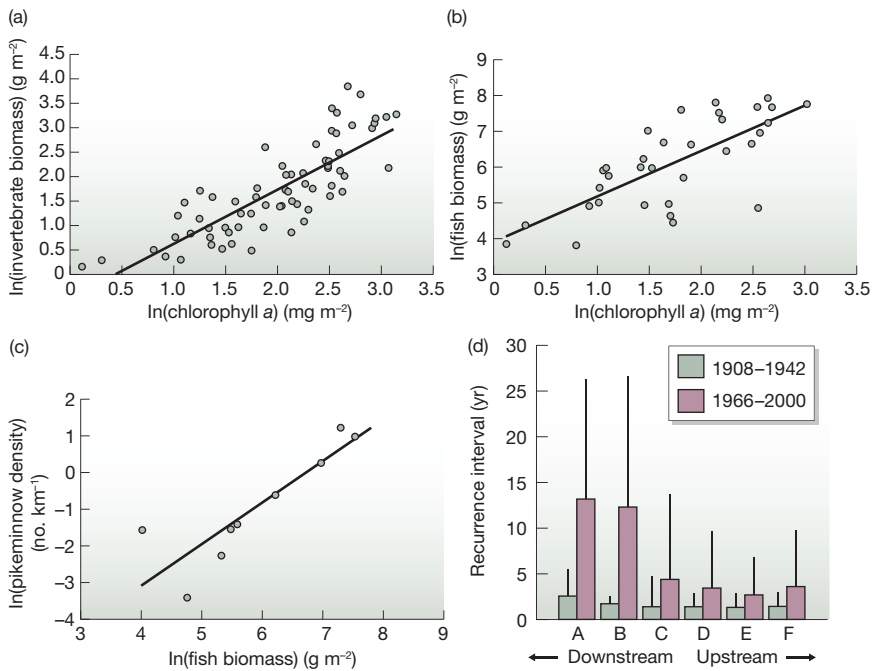
Figure 13.4

Organochlorines, applied as pesticides on land, are transported to the Arctic through river runoff and oceanic and atmospheric circulation. A study in the Barents Sea showed how two classes of pesticide are biomagnified during passage through the marine food chain. Concentrations in sea water are very low. Herbivorous copepods (that feed on phytoplankton) have higher concentrations (measured in nanograms per gram of lipid in the organisms), and predatory amphipods higher concentrations still. The polar cod (*Boreogadus saida*), which feeds on the invertebrates, and cod (*Gadus morhua*) which also includes polar cod in its diet, show further evidence of biomagnification. However, it is the higher steps in the food chain where biomagnification is most marked, because the sea birds that feed on the fish (black guillemots, *Cepphus grylle*) or on fish and other sea birds (glaucous gull, *Larus hyperboreus*) have much less ability to eliminate the chemicals than fish or invertebrates. Note how chlordanes are biomagnified to a lesser extent than polychlorinated biphenyls (PCBs). This results from the birds' greater ability to metabolize and excrete the former class of pesticide.



BASED ON DATA IN BORGÅ ET AL., 2001

The rare Colorado pikeminnow (*Ptychocheilus lucius*), which eats other fish, is now restricted to the upper reaches of the Colorado River. Its present distribution is positively correlated with prey fish biomass, which in turn depends on the biomass of invertebrates upon which the prey fish depend, and this, in its turn, is positively correlated with algal biomass, the energy base of the food web (Figure 13.5a–c). Osmundson et al. (2002) argue that the rarity of pikeminnows can be traced to the accumulation of fine sediment on the riverbed, where it reduces algal productivity in downstream regions of the river. Historically, spring snowmelt often produced flushing discharges with the power to remove much of

**Figure 13.5**

Interrelationships among biological parameters measured in a number of reaches of the Colorado River to determine the ultimate causes of the declining distribution of Colorado pikeminnows. (a) Invertebrate biomass versus algal biomass (chlorophyll *a*). (b) Prey fish biomass versus algal biomass. (c) Pikeminnow density versus prey fish biomass (from catch rate per minute of electrofishing). (d) Mean recurrence intervals in six reaches of the Colorado River (for which historical data were available) of discharges necessary to remove silt and sand that would otherwise accumulate, during recent (1966–2000) and pre-regulation periods (1908–1942). Lines above the histograms show maximum recurrence intervals.

the silt and sand that would otherwise accumulate. As a result of river regulation, however, the mean recurrence interval of such discharges has increased from once every 1.3–2.7 years to only once every 2.7–13.5 years (Figure 13.5d), extending the period of silt accumulation. Managers must aim to incorporate ecologically influential aspects of the natural hydrograph of a river into restoration efforts if endangered (or valuable harvestable) species are to be sustained.

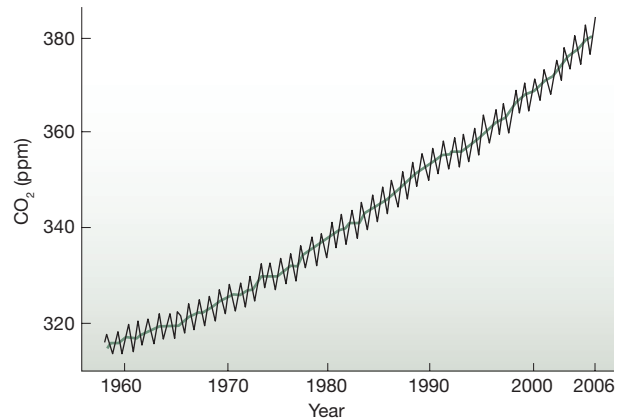
### 13.3 Power generation and its diverse effects

Since the industrial revolution of the 18th century, our use of fossil fuels has provided the power to transform much of the face of the planet through urbanization, industrial development, mining and highly intensive agriculture, forestry and fishing. In Section 13.3.1 we consider the far-reaching effects of chemical pollutants from fossil fuel use. Because fossil fuels are exhaustible, increasingly costly to extract, pollute the atmosphere and contribute to global warming, much recent emphasis has been placed on developing alternative energy sources that do not release carbon dioxide. The cleanest and safest technologies are expected to derive from hydropower schemes (already at a technologically advanced state in many parts of the globe), together with wind farms (rapidly developing) and solar and wave power. Nuclear power, whose popularity had declined because of concerns over security and radioactive waste disposal, is receiving renewed consideration because it does not release greenhouse gases. We discuss nuclear power in Section 13.3.2 and wind power in Section 13.3.3.

**Figure 13.6**

The concentration of atmospheric carbon dioxide measured at the Mauna Loa Observatory, Hawaii showing the seasonal cycle (dipping each northern summer when photosynthetic rates are maximal in the northern hemisphere) and, more significantly, the long-term increase that is due largely to the burning of fossil fuels.

COURTESY OF THE CLIMATE MONITORING AND DIAGNOSTICS LABORATORY (CMDL) OF THE NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION (NOAA)



### 13.3.1 Fossil fuels and atmospheric pollution

The most profound and far-reaching consequences of the burning of fossil fuels, principally coal and oil, are those of atmospheric pollution. Thus, the concentration of carbon dioxide in the atmosphere has increased from about 280 parts per million (ppm) in 1750 to about 370 ppm today, and is projected to continue to rise to 700 ppm by the year 2100 unless there are rather drastic changes in human behavior. A remarkable census of atmospheric carbon dioxide was started in 1958 at Mauna Loa Observatory in Hawaii and this detected the extraordinary pattern shown in Figure 13.6. The principal cause of this increase has been the burning of fossil fuels, which in 1980, for example, released about  $5.2 \times 10^9$  metric tons of carbon into the atmosphere (Table 13.1).

**Table 13.1**

Balancing the global carbon budget (in  $10^9$  metric tons per year) in 1980 to account for increases in atmospheric carbon caused by human activities. In the row labeled 'Missing' the minus sign indicates the need to identify an unknown uptake of carbon of the size shown. This has now been identified as fertilization of terrestrial vegetation by atmospheric carbon dioxide so that an increase of the order of what was estimated as 'missing' can be accounted for by an increase in the amount of carbon locked in extra vegetation biomass (Kicklighter et al., 1999).

	EXTREME LOW ESTIMATE	MEDIAN ESTIMATE	EXTREME HIGH ESTIMATE
<i>Release to atmosphere</i>			
Fossil fuel combustion	4.7	5.2	5.7
Cement production	0.1	0.1	0.1
Tropical forest clearance	0.4	1.0	1.6
Non-tropical forest clearance	-0.1	0.0	0.1
Total release	5.1	6.3	7.5
<i>Accounted for</i>			
Atmospheric increase	-2.9	-2.9	-2.9
Ocean uptake	-2.5	-2.2	-1.8
Missing?	-0.3	+1.2	+2.8

The clearing and burning of tropical forest to make way for agriculture or timber production and the decay of the residues make a further contribution to the increase in atmospheric carbon dioxide (Table 13.1). A considerable amount of this is recaptured in photosynthesis by the replacement vegetation (Kicklighter et al., 1999), but this is least when forest is converted to grassland, which has a much lower biomass. In total about  $1.0 \times 10^9$  metric tons per year has been released through changes in tropical land use (Detwiler and Hall, 1988). This calculation was made for 1980, and the figure for tropical forest clearance must now be significantly greater as a result of the uncontrollable spread of forest fires in Indonesia and in South America following the droughts associated with the El Niño phenomenon of 1997/98.

atmospheric pollution due to the burning of fossil fuels and deforestation

The Earth's atmosphere behaves like a greenhouse. Solar radiation warms up the Earth's surface, which reradiates energy outward, principally as infrared radiation. Carbon dioxide – together with other gases whose concentrations have increased as a result of human activity (nitrous oxide, methane, ozone, chlorofluorocarbons) – absorbs infrared radiation. Like the glass of a greenhouse, these gases (and water vapor) prevent some of the radiation from escaping and keep the temperature high. The air temperature at the land surface is now  $0.6 \pm 0.2^\circ\text{C}$  warmer than in pre-industrial times. Given further predicted rises in greenhouse gases, temperatures will continue to rise by a global average of between  $2.0^\circ\text{C}$  and  $5.5^\circ\text{C}$  by 2100 (IPCC, 2001; Millennium Ecosystem Assessment, 2005), but to different extents in different places. Such changes will lead to a melting of glaciers and icecaps, a consequent rise in sea level, and large changes to global patterns of precipitation, winds, ocean currents and the timing and scale of storm events.

the greenhouse effect

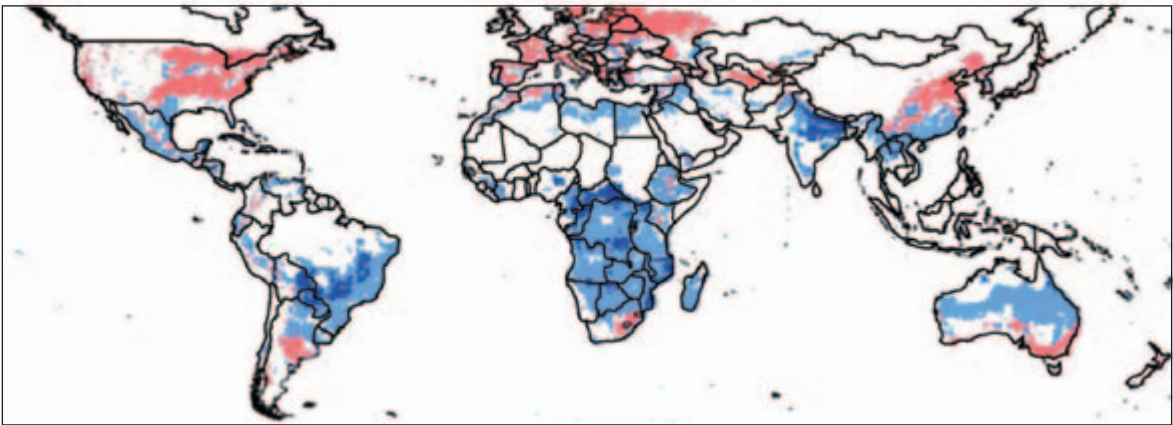
In response to these changes, we can expect latitudinal and altitudinal shifts in species distributions and widespread extinctions as floras and faunas fail to track and keep up with the rate of change in global temperatures (Hughes, 2000). In addition, the global threats imposed by harmful invasive species will change. Take, for example, the Argentine ant (*Linepithema humile*), a native of South America. This is now established on every continent except Antarctica. It can achieve extremely high densities and has adverse consequences for biodiversity (eliminating native invertebrates) and for domestic life, swarming over human foodstuffs and even sleeping babies. A distributional model was developed for the ant, based on occurrences in its native and invaded ranges, and related both to climatic data (e.g. maximum, minimum and mean temperatures, precipitation, number of frost days, number of wet days) and topographic data (e.g. elevation, slope, aspect). The model provided a good fit with current distribution based on current climate. Next, predicted climate change was used to model the ant's future distribution. Figure 13.7 indicates in red those areas predicted to improve for the ant by 2050 (increased likelihood of ant occurrence) and in blue those areas expected to worsen. The species will retract its range in tropical areas but expand into higher latitudes. Ironically, the Argentine ant looks set to do less well in its native South America than in North America and Europe.

Efforts to eradicate Argentine ants have mostly been unsuccessful. The management response is therefore to increase biosecurity precautions in regions expected to become progressively more invadable in future.

Of the pollutants that humans release into the atmosphere, most are returned to Earth, about half as gases or particles and half dissolved or suspended in rain, snow and fog. They may be carried in the wind for hundreds of kilometers across

acid rain





**Figure 13.7**

Predicted changes to the distribution of the Argentine ant between now and 2050. Red areas are those predicted to improve for Argentine ants, whereas blue areas are predicted to worsen for the species.

AFTER ROURA-PASCUAL ET AL., 2004

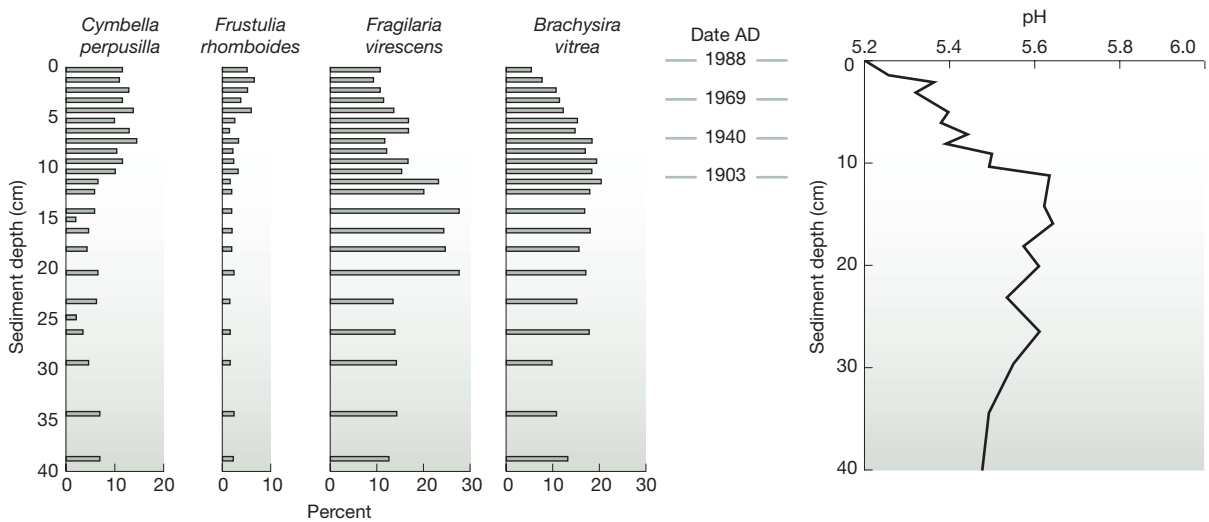
state and national borders, and when they cause harm they can be the source of bitter international dispute. Atmospheric pollutants sulfur dioxide ( $\text{SO}_2$ ) and oxides of nitrogen ( $\text{NO}_x$ ), contributed particularly by the burning of fossil fuels, interact with water and oxygen in the atmosphere to form dilute sulfuric and nitric acids, which fall as *acid rain*.

Rain water has a pH of about 5.6, but pollutants lower it to below 5.0 and values as low as 2.4 have been recorded in Britain, 2.8 in Scandinavia and even 2.1 in the United States. Many of the most visibly dramatic effects of acid rain have been observed in the forests of central Europe where industry depended on low-quality coal with a high sulfur content and forest dieback occurred on a massive scale. Even in the United States, high-elevation spruce forests have been affected, including the Shenandoah and Great Smoky Mountain national parks.

Further effects have occurred in lakes and streams, especially when the composition of the underlying soil and rock does not help to neutralize the acidity. A high concentration of hydrogen ions may itself be toxic, but changes in the availability of nutrients and other toxins are usually more important. At a pH below 4.0–4.5, the concentrations of aluminum ( $\text{Al}^{3+}$ ), iron ( $\text{Fe}^{3+}$ ) and manganese ( $\text{Mn}^{2+}$ ) become toxic to most plants and to aquatic animals that expose delicate tissues directly to the water (such as the gills of fish). Acid rain is most damaging in water that is already naturally acidic: it may then lower the pH so far that it sterilizes the environment for many of the native species (e.g. Figure 13.8).

### 13.3.2 Nuclear power

When first developed, nuclear power was viewed as an almost ideal, long-term source of industrial and domestic power. However, the view that the release of radiation could be readily controlled faded rapidly. Some leakage occurs from nuclear power reactors, and it is doubtful whether the reprocessing of waste



**Figure 13.8**

The history of the diatom flora of an Irish lake (Lough Maam, County Donegal) can be traced by taking cores from the sediment at the bottom of the lake. The percentage of various diatom species at different depths reflects the flora present at various times in the past (four species are illustrated). The age of layers of sediment can be determined by the radioactive decay of lead-210 (and other elements). We know the pH tolerance of the diatom species from their present distribution and this can be used to reconstruct what the pH of the lake has been in the past. Note how the waters have acidified since about 1900. The diatoms *Fragilaria virescens* and *Brachysira vitrea* have declined markedly during this period while the acid-tolerant *Cymbella perpusilla* and *Frustulia rhomboides* increased after 1900.

nuclear fuel can ever be made completely clean. Moreover, the polluting power of radioactive waste has a time scale that may be orders of magnitude greater than that of other human pollutants. For example, plutonium-239 has a half-life of about 25,000 years. Plutonium is separated and recovered from the spent fuel in nuclear reactors and stocks are expected to have risen to more than 100 metric tons by 2010. Ways have to be found to protect against risks of leakage over this sort of time scale, perhaps by burial in deep mines after incorporation in glass.

The radiation received by an organism arises from human activities (nuclear warfare, leakage from and accidents at nuclear plants, and medical use) together with a very similar sized contribution from 'background radiation' from cosmic rays and produced during the radioactive decay of materials such as radium and thorium in the Earth's crust. It is a sobering thought that the total radiation given to a cancer patient can be many thousand times greater than the total normal exposure from the combined natural and artificial background radiation.

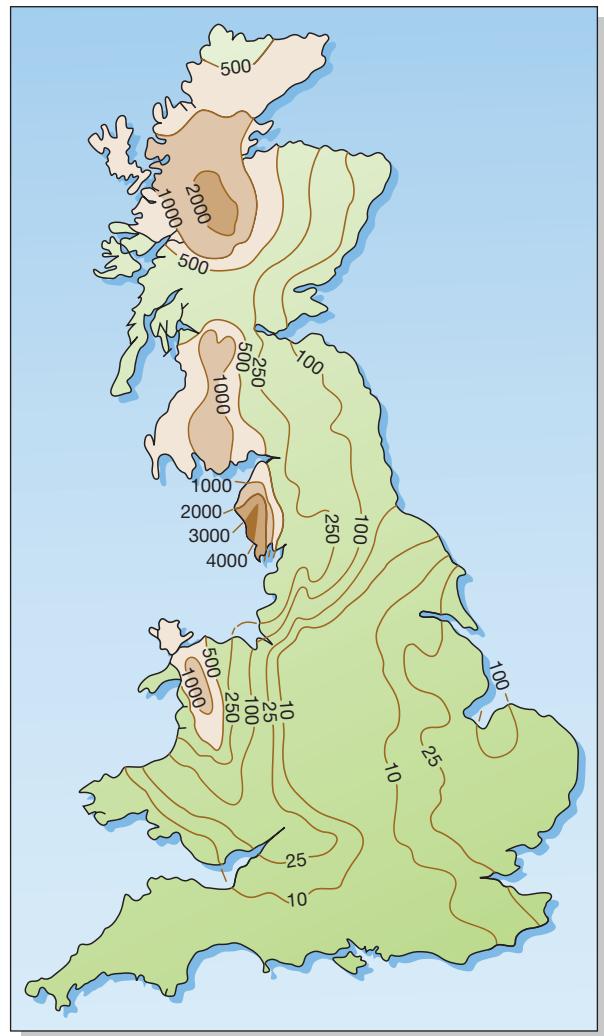
A major accident in 1986 at a nuclear power station at Chernobyl in the Ukraine released 50–185 million curies of radionuclides into the atmosphere. Close to the explosion, 32 deaths occurred within a very short time. Farther away, individuals contracted radiation sickness and some died. Effects in the locality have continued to appear – livestock have been born deformed, and thousands of radiation-induced illnesses and deaths from cancer are expected in the longer term. Farther afield, wind-dispersed atmospheric pollution from Chernobyl was detected in Sweden 3 days after the accident. Fallout also reached the British

natural background radiation and that produced by human activities are of similar magnitude

Chernobyl – the worst nuclear pollution disaster so far

**Figure 13.9**

An example of long-distance environmental pollution: the distribution in 1988 in Great Britain of fallout of cesium-137 from the Chernobyl nuclear accident in the Soviet Union in 1986 (measured in Becquerels per kilogram). The contours show the persistence of the cesium on acidic upland soils where it is recycled through soil, plants and animals. On typical lowland soils, cesium does not persist in food chains.



AFTER NERC, 1990

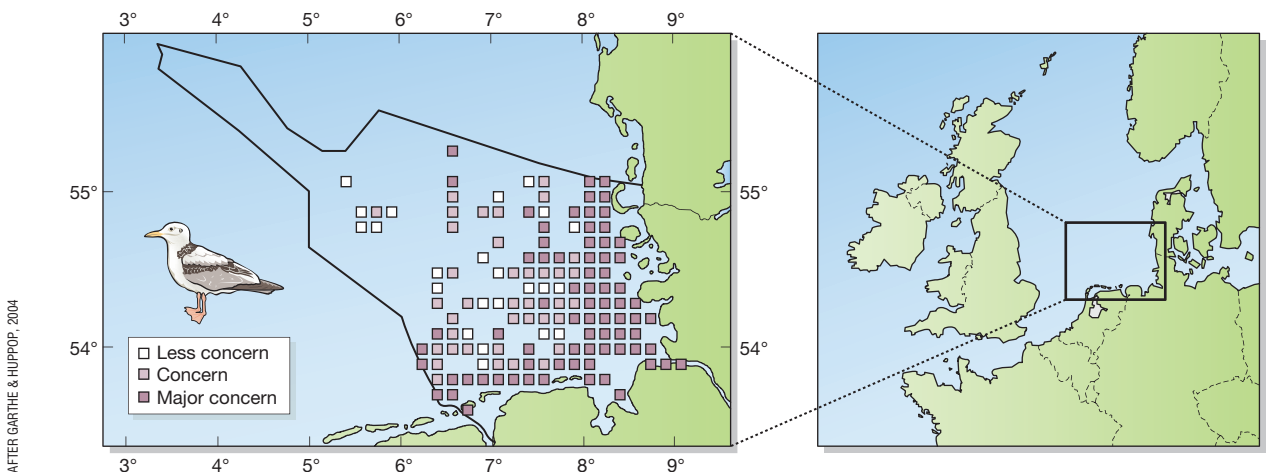
Isles. Figure 13.9 shows the persistence of cesium-137 in the acid soils of the northwest of Britain, where it was absorbed by plants and eaten by sheep. The sale of sheep for food was still banned more than 10 years after the accident because of persistence of the isotope at dangerous levels.

### 13.3.3 Wind power

In this time of global climate change, harnessing the power of the wind has much to commend it. But while this form of power generation does not release carbon dioxide, local communities often object to the massive structures that will appear in their localities. (This conundrum parallels the situation for hydropower stations, which produce clean power but at the cost of altered river discharge patterns and lost recreational opportunities downstream.) Wind farms also pose an ecological risk in terms of threats to migrating birds. On land, soaring birds

such as falcons and vultures are at particular risk of colliding with the turbines (up to 100 m above the ground), particularly because the engineers often select their locations for the same wind-related reasons that birds select their routes (Barrios & Rodriguez, 2004). Many wind farms are also planned for marine settings – in Europe, for example, more than 100 applications have been submitted. Each may consist of as many as 1000 turbines, up to 150 m tall, as far offshore as 100 km and in water as deep as 40 m. The turbines may pose risks to migrating birds (from the smallest of song birds to cranes and birds of prey) as well as sea birds dispersing locally to find food.

Thousands of square kilometres of the marine environment off the German coast are planned for wind farming by 2030. To predict the possible consequences for bird populations, Garthe and Huppop (2004) developed a species sensitivity index (SSI) for 26 seabird species, combining their scores for a range of properties, including flight maneuverability (less agile species score highly because they are more likely to collide with turbines), flight altitude (species flying at 50–200 m score highly because they are more vulnerable to turbines than lower flyers), percentage time spent flying (those in the air for more of the time score highly) and conservation status ('vulnerable' or 'declining' score highly). The most sensitive species (highest SSI) include the non-maneuverable and 'vulnerable' black-throated diver (*Gavia arctica*) and the maneuverable but 'declining' sandwich tern (*Sterna sandvicensis*) that flies almost constantly and at perilous altitudes. The SSI for each species was then coupled with density distribution data (low-density species score highly because their populations are more at risk) to produce vulnerability maps (all bird species combined) for the German area of the North Sea. Three classes of vulnerability were assigned – 'major concern' (combined wind-farm sensitive data [WSI] > 43), 'less concern' (WSI < 24) and 'concern' (between these extremes) (Figure 13.10). Such ecological information should be taken into account when selecting wind farm locations.



**Figure 13.10**

Areas in the German sector of the North Sea (inset, right) where wind farm development is considered to be of 'less concern', 'concern' or 'major concern' on the basis of bird density patterns and species-specific sensitivity indexes (SSIs).

## 13.4 Degradation in urban and industrial landscapes

A wide range of habitat degradation occurs as a result of human activity in urban and industrial settings. Marked changes to riverflow result from the loss of permeable surfaces – roofs, pavements and roads are impermeable, in contrast to field and forest. Our feces, urine and dead bodies create large disposal problems in towns and cities because density is so high. Exotic industrial chemicals find their way into waterways and the atmosphere. And our mining activities, whether for fossil fuels or valuable jewels or ores, cause physical and chemical degradation to surrounding ecosystems. In this section, our examples encompass sewage disposal (Section 13.4.1), the industrial production of fluorocarbons and consequences for the ozone layer (Section 13.4.2) and the ecological problems associated with mining (Section 13.4.3).

### 13.4.1 *Disposal of bodily waste*

All human body products, but most notably feces and urine, can be regarded as pollutants. The Greeks were probably the first to control the accumulation of pollution within towns, and a law of 320 BC forbade dumping of waste in the streets. The Romans were also very pollution conscious, dumping city waste in pits outside the city walls. When Roman and Greek civilizations perished, their quite sophisticated control of urban pollution collapsed. Medieval castles, for example, were often designed with latrines projecting from castle walls that simply dumped waste at the base of the walls (the accumulated wastes give archeologists a direct record of historical diets and infestation with intestinal worms!). Until the 14th and 15th centuries the open streets again became the main, and often the only, destination for human and animal feces and urine. A special trade developed, that of the scavenger, who was paid to carry waste to dumps outside the cities; in 1714 every city in England had an official scavenger (the forerunner of the Environmental Protection Agency!). Even when water closets (invented by Thomas Crapper) began to be installed in some countries early in the 19th century, the underground reservoirs (cesspools) into which they emptied often overflowed and contaminated drinking water. Outbreaks of cholera in the middle of the 19th century were traced directly to this source of contamination, a discovery that led to the connection of household waste directly to sewers in both Britain and the United States.

At first glance, the easiest way to cope with accumulated feces and urine might appear to be to dilute them in large bodies of water. However, it is not easy to dispose of human waste and at the same time provide healthy drinking water. In addition to health issues, we have already seen in Section 13.2.2 how there can be profound ecological effects of disposing of sewage in water bodies.

All natural ecosystems have an inherent capacity to decompose feces and up to a point natural decomposition processes in rivers, lakes and oceans may cope with increased organic matter from human sewage without obvious changes to the nature of the biological communities they contain. However, problems arise when the rate of sewage input exceeds this capacity. First, excessively high rates of decomposition of dead organic matter in rivers and lakes can lead to

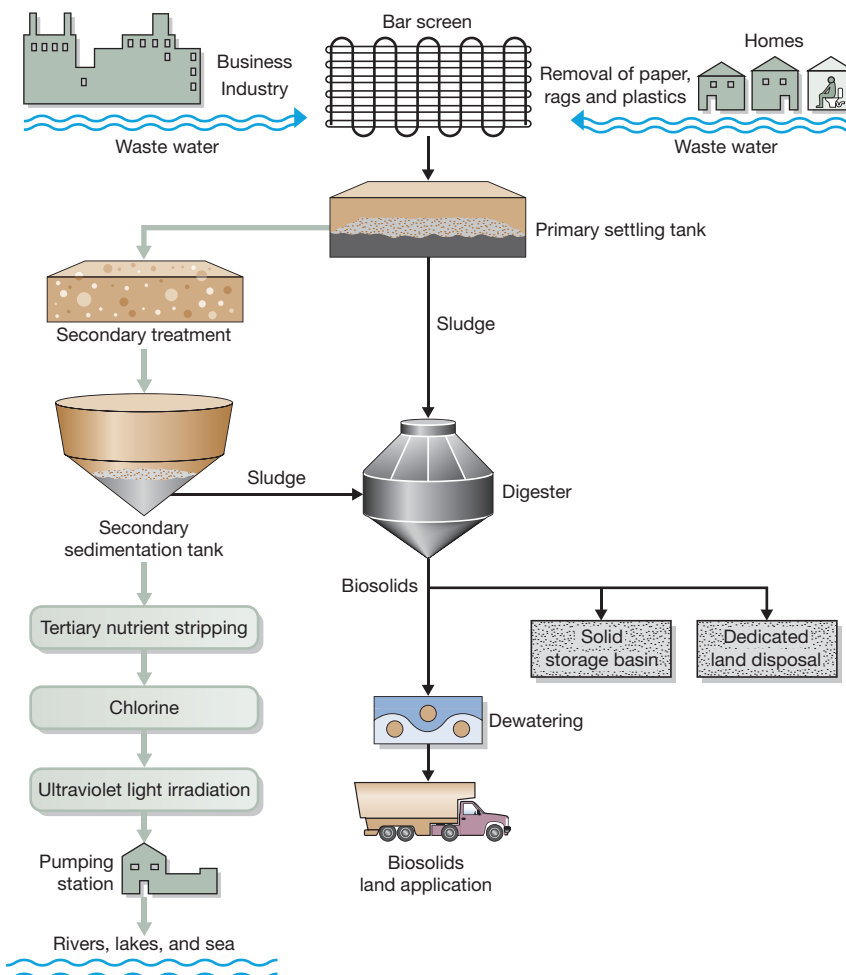
when natural ecosystems cannot cope with human waste . . .

anaerobic conditions (causing the death of fish and invertebrates). This happens because oxygen is consumed by the decomposer microorganisms faster than it is replenished from photosynthesis by aquatic plants and diffusion from the air. Second, the supply of nutrients such as phosphate and nitrate that normally limit plant growth in water bodies may be increased to a level where algal growth is so great that it shades and kills other aquatic plants – the cultural eutrophication discussed in Section 13.2.2.

Modern sewage systems were developed as ecological devices for pollution management. They aim to capture pollutants from waste water and to clean it, usually in a drainage system separate from the one that carries heavy flows of storm water. Ideally, a sewage system cleans polluted water to a state suitable for drinking before discharging it back into rivers, lakes and the sea. The full treatment of sewage has three stages (Figure 13.11), though in many places only the first or first and second stages are actually used before discharge into the environment.

After paper, rags and plastic have been removed by passing the sewage through screens, *primary treatment* is a physical process in which much of the solid

... sewage treatment systems are needed



**Figure 13.11**

The sequence of treatments commonly applied to the sewage waste from a modern urban community.

organic sewage waste is allowed to settle to the bottom of settlement tanks, from which it is removed as sludge.

*Secondary treatment* is an engineered biological process designed to mimic (and indeed enhance) natural decomposition. In its simplest version, the partly cleaned water is sprayed onto a layer of crushed rock within which microorganisms have been encouraged to grow; as the water trickles down through these *percolating* or *trickling filters*, natural decomposition mineralizes much of the remaining organic matter, releasing carbon dioxide to the atmosphere. A more sophisticated and efficient method of secondary treatment is the *activated sludge method*, in which the sewage is passed into aerated tanks containing sludge that is activated, or seeded, with microorganisms. After secondary treatment the remaining solids are settled to yield more sludge. The waste water now appears clean, but it still contains two types of impurity, namely disease organisms and high concentrations of mineral nutrients, the latter having both health consequences (Section 13.2.2) and causing eutrophication if released into rivers and lakes.

A final ‘polishing’ stage usually includes chlorination, and sometimes ultra-violet (UV) light irradiation to kill bacteria. Full *tertiary treatment* involves the stripping of nutrients, largely by artificial and expensive chemical processes.

Untreated sewage is obviously a pollutant, with adverse health and ecological consequences for water bodies into which it is discharged. However, discharge of sewage that has only been subject to primary treatment is still likely to cause eutrophication because it remains rich in organic matter and nutrients. Moreover, even secondary treatment removes only the organic matter, leaving waste water rich in plant nutrients. The sludge that accumulates in settling tanks is itself a pollutant that has to be disposed of, usually by dumping at sea or burying in landfill sites. Buried sludge decomposes anaerobically, sometimes taking more than 20 years to mineralize completely, and it produces methane, which is a greenhouse gas that contributes to global climate change (Section 13.3.1). Sludge can be more appropriately used as a fertilizer, either dried or as a liquid sprayed onto the land; in this way the nutrient cycle can be reconstituted by returning nutrients, assimilated from crops by people, to agricultural land to be taken up by future crops.

products of sewage treatment  
are themselves pollutants

### 13.4.2 Chlorofluorocarbon compounds and thinning of the ozone layer

Ozone is produced by the influence of sunlight on oxygen and during the oxidation of carbon monoxide and hydrocarbons such as methane. It has three very different roles in environmental pollution. The first two are negative, in the sense that undesirable polluting consequences occur as the concentration of ozone increases. First, in atmospheres polluted with methane, industrial hydrocarbons, oxides of nitrogen and carbon monoxide, ozone can reach concentrations that are toxic to plants and that contribute to smog. Second, ozone is also a greenhouse gas, though it is not particularly significant in this respect.

However, ozone also accumulates as a layer in the upper atmosphere. This ‘ozone layer’ is beneficial because it absorbs most of the UV radiation (wavelength 200–300 nm) incident on the Earth’s upper atmosphere and so makes the Earth habitable for plants and animals. The increasing frequency of skin cancer among humans has focused attention on the damage caused by exposure to the sun and on the importance of stability of the ozone layer.

ozone can have adverse  
consequences locally . . .

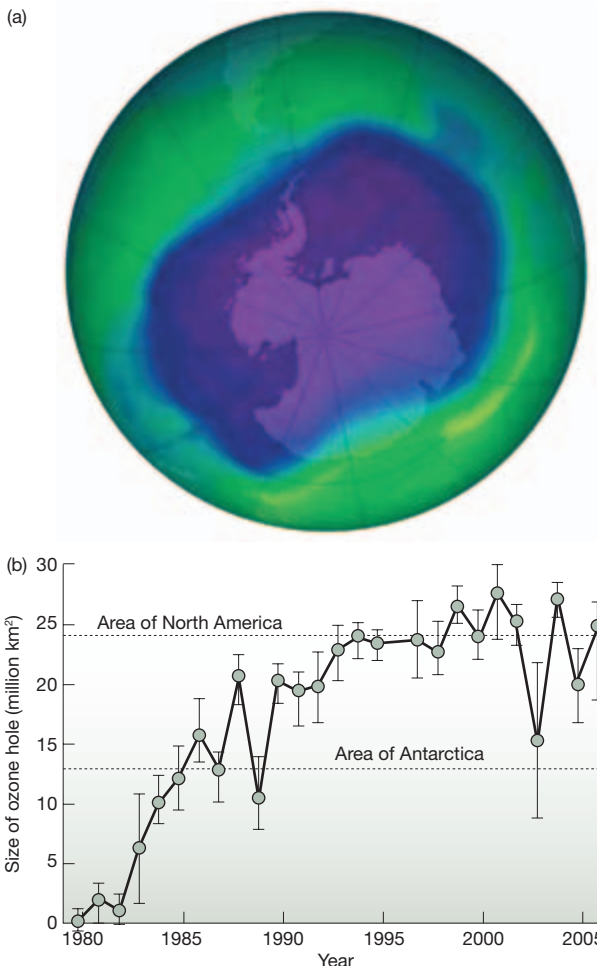
. . . but in the upper atmosphere  
it shields the Earth from  
damaging UV radiation



Evidence that nitric oxide produced by supersonic aircraft might contribute massively to reduce the level of atmospheric ozone led to the halting of their large-scale development. However, that has by no means been the end of the story. Chlorofluorocarbon compounds (CFCs) had been developed as aerosols and refrigerants and used on a very large, international scale. It became clear that these posed the threat that their chlorine content could interact with and destroy atmospheric ozone.

Ozone chemical processes are very complicated, and methane, nitrous oxide and carbon monoxide may all play a part in its decomposition. The upper atmosphere is not the easiest place in which to study the chemical characteristics of gases! But pollution of the upper atmosphere poses questions of the greatest significance for environmental scientists, especially since the discovery that the concentration of ozone in the atmosphere over Antarctica had started to decline by 1978 and was doing so very rapidly after 1982. The phenomenon happens at the start of the southern hemisphere spring (August to October). The size of the ozone hole over Antarctica on September 24, 2006 was one of the largest ever recorded, equivalent to more than the surface area of North America (Figure 13.12). It is

chlorine compounds and other pollutants decompose ozone in the atmosphere and need to be phased out



**Figure 13.12**

(a) An image of the ozone hole over Antarctica for September 24, 2006; the blue and purple colors are where there is least ozone (<220 Dobson units). (b) Average size of the ozone hole from September 7 to October 13 each year from 1980 to 2006. The vertical lines show the minimum and maximum areas during this period each year.

clearly in the interests of humans and probably most other organisms that ozone concentrations should remain low close to the Earth's surface (e.g. minimizing smog) but high in the upper atmosphere, and that we should find out how to ensure this. International agreements to phase out CFCs are expected to lead to recovery of the ozone hole by about 2050.

### 13.4.3 Mining

physical disruption from the mining of fossil fuels

Our dependence on fossil fuels has effects that go beyond atmospheric pollution. The extraction and transport of coal and especially oil can also cause physical disruption of habitats. Thus, more than 1 million tonnes of oil enters the world's waterways every year from wells drilled into the seabed or from oil tankers. Oil in and on the sea affects wildlife in many ways. It reduces the level of aeration of the water, and it prevents light from penetrating the surface. Damage to invertebrates can be widespread, affecting chitons, mussels, crustaceans and bryozoans, as well as seaweeds and kelps. Feathers become choked with oil so that sea birds cannot fly and fish gills become coated and cease to function. The largest accident in the United States occurred on March 24, 1989, when the oil tanker *Exxon Valdez* ran aground in Prince William Sound, Alaska. It spilled nearly 50,000 tons of crude oil, which spread along the coast for nearly 1000 km, contaminating the shores of a national forest, five state parks, four state critical habitat areas and a state game sanctuary. The episode is believed to have killed 300 harbor seals, 2800 sea otters, 250,000 birds and possibly 13 killer whales. Many commercial fisheries were closed for a year or more because of the concern that fish caught in the area might find their way into the human food chain. By 1996, 28 species and resources were still listed as having failed to recover.

the mining and purification of copper

Metals were first used by humans in the late Stone Age, about 6500 years ago. Gold, silver and copper were the first metals used; they are easy to extract because they exist in nature as the metals themselves rather than as chemical compounds. Nuggets of pure metallic gold were found in riverbeds and were beaten and molded for decoration. Once such metals were valued it was an obvious step to dig and mine for them, and from that point almost every phase in the extraction and industrial use of metals involves a sequence of phases of environmental pollution.

Each type of metal has its own peculiarities. Here we use the mining and purification of copper to illustrate pollution through the extraction of metal. Copper is present in deposits either as the metal or as copper sulfide or oxide. Like most metal deposits, it usually exists in a mixture with other metals, some of which may be worth saving (e.g. gold), whereas others are discarded in more or less hazardous waste.

The mining industry may pollute at every stage of extraction, purification and disposal:

- 1 Mining and quarrying. Mining or quarrying exposes the metal and its ores. Many of the world's copper reserves are close to the surface and are easily extracted by open cast mining: the copper mines of Bougainville (Solomon Islands, Papua New Guinea) and of Utah are among the largest human scars on the Earth's surface (Figure 13.13).

**Figure 13.13**

Binyon Canyon Mine, Utah. A toxic and sterile environment created by the world's largest excavation.

© DAVID R. FRAZIER

- 2 Processing. The ores are crushed and finely ground. This processing immediately exposes ores to the elements, and even after the best has been extracted the residues are copper-rich and the metal leaches as toxic waste into rivers and lakes. Waters close to copper mines are commonly brilliantly blue-green with copper salts and quite sterile.
- 3 Concentration. The finely ground ore is agitated in water, and the metal becomes concentrated in the froth and dried to a cake. The remainder, which is still rich in copper, may be further concentrated to recover more of the metal. Ultimately water and solid 'tailings' have insufficient copper to warrant further extraction but contain sufficient copper to form a hazardous and polluting waste.
- 4 Purification through heat. The concentrate is then roasted to 1230–1300°C, polluting the atmosphere by the burning of the necessary fuel. The roasting drives off a host of pollutants such as arsenic, mercury and sulfur into the atmosphere.
- 5 Purification through electrolysis. The copper can now be purified by electrolysis, which leaves most of the other metals in a sludge that may be further purified (to remove gold, for example) but ultimately contributes yet more toxic waste.

The major role of some metals as environmental pollutants occurs after they have been purified and used industrially and are then released into the environment as industrial waste. Lead and mercury are particularly striking examples. Lead became an environmental pollutant from the moment that the Romans started to use it to make water pipes and so started to pollute their drinking water. It is ranked by the US Environmental Protection Agency as number 1 in their list of 275 hazardous substances, posing a particular risk for the development of the nervous system in young children and in the fetus. It is being phased out of many commercial uses.

lead and mercury can be especially dangerous pollutants

It is not clear whether lead pollution has significant consequences for wildlife on the land or in aquatic environments, but it does not appear to become concentrated along food chains. This is a major contrast with mercury.

Mercury is used in a variety of specialized applications in industry and medicine – in electric switches, batteries, fluorescent and mercury vapor lights, thermometers, barometers and dental amalgams. The main culprits in releasing mercury to the atmosphere are, in order of importance, coal-fired power plants, medical waste incinerators, municipal waste incinerators and industrial boilers. In the natural environment mercury can be converted by microbial activity to methylmercury, a form that is readily absorbed and accumulated up food chains, especially in lakes and estuaries. Fish, the top predators, may accumulate concentrations of mercury 10,000 to 100,000 times that in the surrounding water (Bowles et al., 2001). Native peoples who hunt and eat wildlife can accumulate even higher concentrations. Mercury is a serious poison that can cause permanent damage to the human brain and kidneys, and particularly to the developing fetus. It may also damage the immune system.

prospecting for plant species to restore contaminated sites

Land that has been damaged by mining is usually unstable, liable to erosion and devoid of vegetation. The simplest solution to land reclamation is the re-establishment of vegetation cover, because this will stabilize the surface, be visually attractive and self-sustaining (Bradshaw, 2002). Candidate plants for reclamation are those that are tolerant of the toxic heavy metals present. Of particular value are ecotypes – different genotypes, within a species, that fill different niches (see Section 2.3.1) – that have evolved resistance in mined areas. Thus, certain metal-tolerant grass genotypes (or cultivars) have been selected for commercial production in the UK for use on neutral to alkaline soils contaminated by acidic copper wastes (*Agrostis capillaris* cultivar ‘Parys’) or lead or zinc (*Festuca rubra* cultivar ‘Merlin’) (Baker, 2002).

In addition, many species characteristic of naturally metal-rich soils have evolved biochemical systems for nutrient acquisition, detoxification and the control of local geochemical conditions. *Phytoremediation* of metal-contaminated sites can take a variety of forms (Susarla et al., 2002). *Phytoaccumulation* occurs when the contaminant is taken up by the plants but is not degraded rapidly or completely; these plants, such as the zinc-accumulating herb *Thlaspi caerulescens*, are harvested to remove the contaminant and then replaced. *Phytostabilization*, on the other hand, takes advantage of the ability of root exudates to precipitate heavy metals and render them biologically harmless. Finally, *phytotransformation* involves elimination of a contaminant by the action of plant enzymes; for example, hybrid poplar trees *Populus deltoides* × *nigra* have the remarkable ability to degrade TNT (trinitrotoluene) and show promise for the restoration of munition dump areas.

## 13.5 Maintenance and restoration of ecosystem services

a triple bottom-line approach to natural resource management

We have now considered a range of examples of the many impacts of human activities on ecosystems, noting that these can often be measured in terms of lost ‘ecosystem services’ (Section 13.1.2). The concept of ecosystem services brings

into focus three very different ways of looking at our effects on the natural world. First, there are the *environmental* outcomes – the realm of the ecologist. But there are also *economic* and *sociopolitical* perspectives. In this section we explore this triple bottom-line approach to sustainable natural resource use by considering two examples – one at a regional scale (Section 13.5.1) and the other global (Section 13.5.2).

### 13.5.1 Managing an agricultural landscape

When farm production becomes too intensive and widespread, biodiversity is lost because of the loss of species-rich habitat remnants and the impact of high levels of pesticides. At the same time there is an adverse effect on ecosystem services, such as the provision of water of high quality for drinking and contact recreation. Normally provided ‘free’ from a healthy landscape, these can be lost because of the input of large quantities of nitrogen and phosphorus, fine sediment from eroding land, and an increase in water-borne pathogens from farm animals that affect humans (such as the *Giardia* parasite).

The impact of agriculture depends on the proportion of the landscape that is used for production. One small farm – even if there is excessive use of plow, fertilizer and pesticide – will have little effect on biodiversity and water quality in the landscape as a whole. It is the cumulative effect of larger and larger areas of intensive agriculture that depletes the region’s biodiversity and reduces the quality of water needed for other human activities. In other words, management of agricultural landscapes needs to be done at a regional scale.

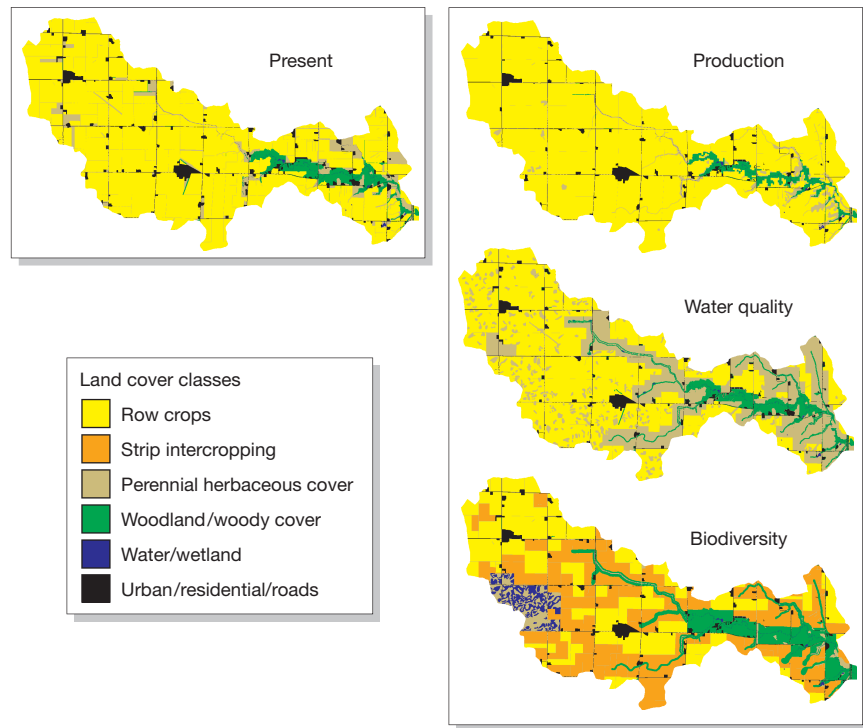
Santelmann et al. (2004) integrated the knowledge of experts in environmental, economic and sociological disciplines into alternative visions of a particular landscape – the catchment area of Walnut Creek, in an intensively farmed part of Iowa, USA. They mapped the present pattern of land use and then created three future management strategies, assessing how farm income, water quality and biodiversity would be expected to change under each scenario. A *production* scenario imagines what the catchment will look like in 25 years if continued priority is given to corn and soybean production (‘row’ crops), following a policy that encourages extension of cultivation to all the highly productive soils available in the catchment. A *water quality* scenario envisions a new (hypothetical) federal policy that enforces chemical standards for river and ground water, and supports agricultural practices that reduce soil erosion. And a *biodiversity* scenario assumes a new (hypothetical) federal policy to increase the abundance and richness of native plants and animals – in this case a network of biodiversity reserves is established with connecting habitat corridors (including the riparian zones of rivers).

Figure 13.14 compares for the three scenarios the distribution of agricultural and ‘natural’ habitats in 25 years’ time. Compared with the current situation, the ‘production’ scenario produces the most homogeneous landscape, with an increase in row crops and a decrease in the less profitable pasture and forage crops. The ‘water quality’ scenario leads to more extensive riparian strips of natural vegetation cover and more perennial crop cover (pasture and forage crops), which are conducive to both higher water quality and biodiversity. Finally, the ‘biodiversity’ scenario has even wider riparian strips together with prairie, forest and wetland reserves, and an increase in strip intercropping, a

comparing three scenarios for managing a catchment area

**Figure 13.14**

Present landscape (top left) and alternative future scenarios for the Walnut Creek catchment area in Iowa, USA. In comparison to the current situation, note how row crops increase at the expense of perennial cover in the 'production' scenario. In the 'water quality' scenario, note the increase in perennial cover (pasture and forage crops) and wider riparian buffers. In the 'biodiversity' scenario, note the increase in strip intercropping, the wide riparian buffers and the extensive prairie, forest and wetland restoration reserves.



FROM SANTELMANN ET AL., 2004

farmers accept a 'biodiversity' scenario despite lower productivity

farming practice that benefits biodiversity because it increases connectivity between reserves.

The percentage change after 25 years in economic, water quality and biodiversity terms is shown for each scenario in Figure 13.15. Not surprisingly, the 'biodiversity' scenario ranks highest for improvements in plant and animal biodiversity. More unexpected is the finding that the land use and management practices required by the 'biodiversity' scenario are nearly as profitable to farmers as current practices. The 'biodiversity' scenario also ranks highest in terms of acceptability to farmers (based on farmer ratings of images of land cover under each scenario), and provides water quality improvements similar in magnitude to those in the 'water quality' scenario. Despite the slightly higher profitability of the 'production' scenario, it seems that the farmers would not be unhappy with a 'biodiversity' strategy that provides the greatest benefits to the community at large in terms of biodiversity and ecosystem services.

### 13.5.2 Global environmental outcomes of different sociopolitical scenarios

Dealing with the diversity of views among neighbors in a farming region is difficult enough, but our biggest environmental problems require a multinational, global change to the way we deal with nature.

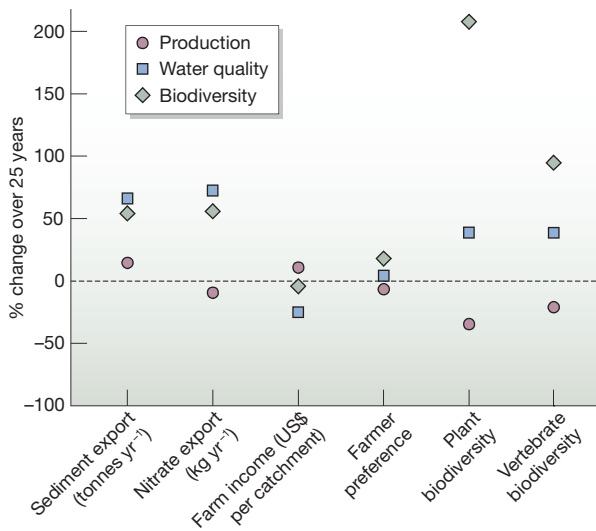


Figure 13.15

Percent change in the Walnut Creek catchment area for each scenario ('production', 'water quality' and 'biodiversity', compared to the current situation) in water quality measures (sediment, nitrate concentration), an economic measure (farm income in the catchment as a whole), a measure of farmer preference for each scenario (based on farmer ratings of images of what the land cover would look like under each scenario) and two biodiversity measures (plant and vertebrate). The 'biodiversity' and 'water quality' scenarios rank above the 'production' scenario in all but economic profitability.

An analysis of four contrasting sociopolitical scenarios in Table 13.2 explores likely trends in climate change, pollution problems and the state of ecosystem services. If there is little change in our sociopolitical outlook – that is, if our world remains regionalized and fragmented and mainly concerned with security and protection – the *order from strength* scenario is expected to apply, with poor economic growth, degradation of all ecosystem services and a large increase in global temperature. A more globally connected society (*global orchestration*) could produce higher economic growth and the biggest improvement for the poorest people, but at the cost of many ecosystem services and with the largest predicted temperature increase (particularly because of continued heavy fossil fuel use). The scenario *adapting mosaic*, of a world driven by local communities focusing on sound environmental management (such as our regional example in Section 13.5.1) would lead to the smallest economic growth, improvements to all ecosystem services and an intermediate rise in global temperature. Finally, the *technogarden* scenario, with its environmentally sound but highly managed ecosystems, and crucially with a climate change policy (stabilizing carbon dioxide at 550 ppm), leads to the smallest rise in temperature, reduces nutrient pollution of waterways and improves ecosystem services – except cultural ones, because many ecosystems are managed and unnatural.

Which of these, or other, scenarios comes to pass depends on a wide range of sociopolitical factors. Watch this space!



**Table 13.2**

Four scenarios that explore plausible futures for ecosystems and human well-being based on different assumptions about sociopolitical forces of change and their interactions. Greenhouse gas emissions [carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>), nitrous oxide (N<sub>2</sub>O) and 'Other'] are expressed as gigatons of carbon-equivalents (GtC-eq).

	GREENHOUSE GAS EMISSIONS TO 2050	PREDICTED TEMPERATURE RISE TO 2050 AND 2100	LAND USE CHANGES TO 2050	NITROGEN TRANSPORT IN RIVERS TO 2025	ECOSYSTEM SERVICES TO 2025
<b>Global orchestration</b> A globally connected society focused on global trade and economic liberalization. Assumes a reactive approach to ecosystem problems. Takes strong steps to reduce poverty and inequality and to invest in public goods such as infrastructure and education. Economic growth is the highest of the four scenarios, while population in 2050 is lowest (8.1 billion)	CO <sub>2</sub> : 20.1 GtC-eq CH <sub>4</sub> : 3.7 GtC-eq N <sub>2</sub> O: 1.1 GtC-eq Other: 0.7 GtC-eq	2050: +2.0°C 2100: +3.5°C	Slow forest decline to 2025, 10% more arable land	Increased nitrogen in rivers	Provisioning services improved, regulating and cultural services degraded
<b>Order from strength</b> A regionalized and fragmented world, concerned with security and protection, emphasizing primarily regional markets, paying little attention to public goods and taking a reactive approach to ecosystem problems. Economic growth rate is the lowest (particularly in developing countries) while population growth is the highest of the scenarios (9.6 billion in 2050)	CO <sub>2</sub> : 15.4 GtC-eq CH <sub>4</sub> : 3.3 GtC-eq N <sub>2</sub> O: 1.1 GtC-eq Other: 0.5 GtC-eq	2050: +1.7°C 2100: +3.3°C	Rapid forest decline to 2025, 20% more arable land	Increased nitrogen in rivers	All ecosystem services heavily degraded
<b>Adapting mosaic</b> River catchment-scale ecosystems are the focus of political and economic activity. Local institutions are strengthened and local ecosystem management strategies are common, with a strongly proactive (and learning) approach. Economic growth is low initially but increases with time. Population in 2050 is high (9.5 billion)	CO <sub>2</sub> : 13.3 GtC-eq CH <sub>4</sub> : 3.2 GtC-eq N <sub>2</sub> O: 0.9 GtC-eq Other: 0.6 GtC-eq	2050: +1.9°C 2100: +2.8°C	Slow forest decline to 2025, 10% more arable land	Increased nitrogen in rivers	All ecosystem services improved
<b>Technogarden</b> A globally connected world relying on environmentally sound technology, using highly managed, often engineered, ecosystems to deliver ecosystem services, and taking a proactive approach to ecosystem management. Economic growth is relatively high and accelerating, while the 2050 population is midrange (8.8 billion). This is the only scenario to assume a climate policy (stabilizing CO <sub>2</sub> at 550 ppm)	CO <sub>2</sub> : 4.7 GtC-eq CH <sub>4</sub> : 1.6 GtC-eq N <sub>2</sub> O: 0.6 GtC-eq Other: 0.2 GtC-eq	2050: +1.5°C 2100: +1.9°C	Forest increase to 2025, 9% more arable land	Decreased nitrogen in rivers	Provisioning and regulating services improved, cultural services degraded



## Summary

### SUMMARY

#### Physical and chemical impacts of human activities

People physically degrade or chemically pollute natural ecosystems when generating power or developing land for agricultural, urban and industrial purposes. Humans are not unique among species in degrading their environment, and when our population density was low, and prior to our harnessing of non-food energy, humans probably had no greater impact than many other species. But now the scale of human effects is proportional to our huge numbers and advanced technologies.

Habitat degradation has costs in terms of human health and lost ecosystem services, including provisioning services (such as wild foods and drinking water), cultural services (including educational and recreational opportunities), regulating services (such as the ecosystem's ability to break down pollutants or regulate climate) and supporting services (including primary production and soil formation).

#### Degradation via cultivation

The intensive production of livestock in factory farming is seriously polluting, and agricultural slurry may need to be thinly dispersed over extensive farmland to dilute it to a level that natural decomposers can deal with it. Intensive agriculture is associated with an increase in the nitrate and phosphate that runs into rivers, lakes and oceans. The consequent eutrophication may be counteracted by matching fertilizer supply to crop demand, restoring natural wetlands (or constructing artificial ones) to take up some of the excess nutrients before they enter rivers and, in lakes, by biomanipulating the level of grazing on phytoplankton to increase water clarity.

Many manufactured pesticides have become important environmental pollutants. Problems arise when pesticides are toxic to many more species than just the target and particularly when they drift beyond the target areas and persist in the environment. The organochlorine insecticides have been particularly problematic because they are progressively biomagnified in animals further up the food chain. Top

predators in aquatic and terrestrial food chains, which were never intended as targets, can then accumulate very high doses.

Cultivation can also physically degrade a landscape through the loss of habitat diversity, while heavy irrigation depletes water in rivers and changes their patterns of flow, with adverse consequences for river inhabitants.

#### Power generation and its diverse effects

Our use of fossil fuels has provided the power to transform much of the face of the planet through intensive agriculture, urbanization and industrial development. The polluting effects of burning coal and oil include acid rain, which can affect lakes and forests in neighboring countries, and a dramatic increase in atmospheric carbon dioxide, which is responsible for climate change at the global level.

Recent emphasis has been placed on developing alternative energy sources that do not release carbon dioxide. The cleanest and safest technologies are expected to derive from hydropower schemes (already at a technologically advanced state in many parts of the globe), together with wind farms (rapidly developing, but with potential adverse consequences for migrating birds) and solar and wave power. Nuclear power, whose popularity had declined because of concerns over security and radioactive waste disposal, is receiving renewed consideration because it does not release greenhouse gases.

#### Degradation in urban and industrial landscapes

Our feces and urine create large disposal problems in towns and cities because density is so high. At its simplest, primary sewage treatment simply removes most of the solid organic matter. Secondary treatment mimics natural decomposition processes, eliminating organic matter but leaving high concentrations of nitrate and phosphate in the waste water. Tertiary treatment chemically removes these nutrients.

Exotic industrial chemicals also find their way into waterways and the atmosphere where they cause diverse problems. For example, chlorofluorocarbon compounds (CFCs), developed as aerosols and

refrigerants and used on a very large international scale, were found to pose the threat that their chlorine content could interact with and destroy atmospheric ozone, which normally protects the world's biota from harmful UV radiation. International agreement to phase out CFCs is expected to solve the problem by 2050 (including recovery of the substantial ozone hole that forms annually over Antarctica).

Mining activities, whether for fossil fuels or metals, also cause physical and chemical degradation to surrounding ecosystems. For example, more than 1 million tonnes of oil enters the world's waterways every year from wells drilled into the seabed or from oil tankers, with adverse consequences for marine life. Mining for metals such as copper may also pollute at every stage of extraction, purification and disposal.

Land that has been damaged by mining is usually unstable, liable to erosion and devoid of vegetation. The simplest solution to land reclamation is the re-establishment of vegetation cover, because this will stabilize the surface, be visually attractive and self-

sustaining. Candidate plants for reclamation are those that are tolerant of the toxic heavy metals present.

### Maintenance and restoration of ecosystem services

The concept of ecosystem services brings into focus three very different ways of looking at our effects on the natural world – the triple bottom-line of environmental, economic and sociopolitical perspectives. Planning for sustainable use of natural resources usually needs to be carried out at regional or global scales.

The impact of agriculture depends on the proportion of the landscape that is used for production, and planning needs to be done at the regional scale and involve the knowledge of experts in environmental, economic and sociological disciplines. Dealing with the diversity of views among neighbors is difficult enough, but our biggest environmental problem – climate change due in large measure to the burning of fossil fuels – requires a multinational, global level of planning.

## Review questions

### REVIEW QUESTIONS

Asterisks indicate challenge questions

- 1 What are the features that distinguish human pollution of the environment from that by other social organisms?
- 2 Explain why it may be impossible to achieve increasing agricultural production without creating unacceptable levels of nitrate in drinking water.
- 3\* Consider the toilet that you most frequently use. Find out where your sewage goes and how it is treated. What pollution problems are you contributing to as a result of your sewage disposal?
- 4 Describe the causes of acid rain and the way in which it damages terrestrial and aquatic communities.
- 5\* Hydroelectric schemes provide one of the least polluting ways of generating power.
- 6 Define the characteristics that make some pesticides particularly dangerous pollutants.
- 7 Describe the ways in which the use of metals by humans has created problems of environmental pollution.
- 8 Define the greenhouse effect and list the pollutants that contribute to it.
- 9\* Review the case of the Asian vultures heading to extinction (see Section 1.3.4) and describe the ecosystem services that would be lost with the vultures. In outline, describe how economic value could be estimated for these services.
- 10\* It is often argued that environmental pollution can be prevented only by 'making the polluter pay'. Discuss the ways in which this is, or might be, done.

# Chapter 14



## Conservation

### *Chapter contents*

#### CHAPTER CONTENTS

- 14.1 Introduction
- 14.2 Threats to biodiversity
- 14.3 Conservation in practice
- 14.4 Conservation in a changing world
- 14.5 Finale

### *Key concepts*

#### KEY CONCEPTS

In this chapter you will:

- recognize that in seeking to conserve the Earth's species and communities, we are often woefully ignorant of what there is to conserve
- appreciate that endangered species are usually rare, but not all rare species are endangered
- understand that some species are at risk for a single reason, such as overexploitation, habitat disruption or introduced species, but often a combination of factors is at work
- recognize that populations that become very small may experience genetic problems
- understand that conservation involves the development of species management plans but also often requires a broader, community perspective
- appreciate that global climate change further complicates conservation planning

*Natural ecosystems have been placed at threat by a plethora of human influences, particularly in the face of a burgeoning human population. Conservation is the science concerned with increasing the probability that the Earth's species and communities (or, more generally, its biodiversity) will persist into the future. We need to appreciate the scale of the problem, understand the threats posed by human activities and consider how our knowledge of ecology can be brought to bear to provide remedies.*

## 14.1 Introduction

what is biodiversity?

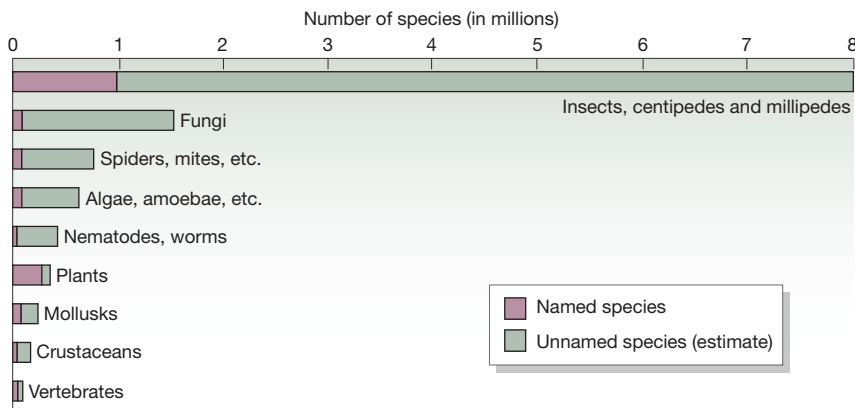
The term *biodiversity* makes frequent appearances in both the popular media and the scientific literature – but it often does so without an unambiguous definition. At its simplest, it is species richness, the number of species present in a defined geographic unit (see Chapter 10). Biodiversity, though, can also be viewed at scales smaller and larger than the species. For example, we may include genetic diversity within species, perhaps seeking to conserve genetically distinct subpopulations and subspecies (see Chapter 8). Above the species level, we may wish to ensure that species without close relatives are afforded special protection, so that the overall evolutionary variety of the world's biota is maintained as large as possible. At a larger scale still, we may include in biodiversity the variety of community types present in a region – swamps, deserts, early and late stages in a woodland succession and so on. Thus, 'biodiversity' may itself, quite reasonably, have a diversity of meanings. Yet it is necessary to be specific if the term is to be of any practical use. Ecologists must define precisely what it is they mean to conserve in their particular circumstances, and how to measure whether this has been achieved.

estimates of the number of species on Earth range from 3 to 30 million or more

Most often the focus of concern of conservation biologists is the rate of extinction of species in the face of human influence. To judge the scale of this problem, we need to know the total number of species that occur in the world, the rate at which these are going extinct and how this rate compares with that of pre-human times. Unfortunately, there are considerable uncertainties in our estimates of all these things. About 1.8 million species have so far been named (Figure 14.1), but the real number must be much larger. Estimates have been derived in a variety of ways. One approach, for example, uses information on the rate of discovery of new species to project forward, group by taxonomic group, to a total estimate of up to 6–7 million species in the world. However, the uncertainties in estimating global species richness are profound and our best guesses range from 3 to 30 million or more (Gaston, 1998).

modern extinction rates compared to historical extinction rates

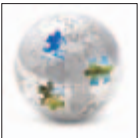
An important lesson from the fossil record is that the vast majority of (probably all) species eventually become extinct – more than 99% of species that ever existed are now extinct. However, given that individual species are believed, on average, to have lasted about 1–10 million years, and if we estimate conservatively that the total number of species on Earth is 10 million, we would predict that only an average of between 100 and 1000 species (0.001–0.01%) would go extinct each

**Figure 14.1**

Numbers of species identified and named (maroon histograms) and estimates of unnamed species that exist (green histograms).

century. The current observed rate of extinction of birds and mammals of about 1% per century is 100–1000 times this ‘natural’ background rate. Furthermore, the scale of the most powerful human influence, habitat destruction, continues to increase.

The evidence, then, while inconclusive to a degree because of the unavoidable difficulty of making accurate estimates, suggests that our children and grandchildren may live through a period of species extinction comparable to the ‘natural’ mass extinctions evident in the geological record (see Section 10.6). But should we care? To most, the answer is a resounding and unhesitating ‘Yes’. Whether the answer seems obvious or debatable, however, it is important to consider *why* we should care – *why* biodiversity is valuable (Box 14.1).



## 14.1 Topical EConcerns

### What is the value of biodiversity?

To most people, biological diversity is undeniably of value but standard economics has generally failed to assign value to ecological resources. Thus, the costs of environmental damage or depletion of living resources have frequently been disregarded. A major challenge is the development of a new *ecological economics* (Costanza et al., 1997) in which the worth of species, communities and ecosystems can be assigned financial value to be set against the gains to be made in industrial and other human projects that may damage them. As we saw in Section 13.1.2, the value of biodiversity can be measured in terms of the ‘free’ *ecosystem services* it provides.

Many species have direct value and many more are likely to have a potential value that as yet remains untapped. For example, wild meat, fish and plants remain vital resources in many parts of the world, while most of the world’s food is derived from plants that were originally domesticated from wild plants in tropical and semiarid regions. In future, wild strains of these species may be exploited for their genetic diversity, and quite different species of plants and animals may be found that are appropriate for domestication. Secondly, as we saw in Chapter 12, the potential benefits that might come from natural enemies if they could be used as biological control agents for pest



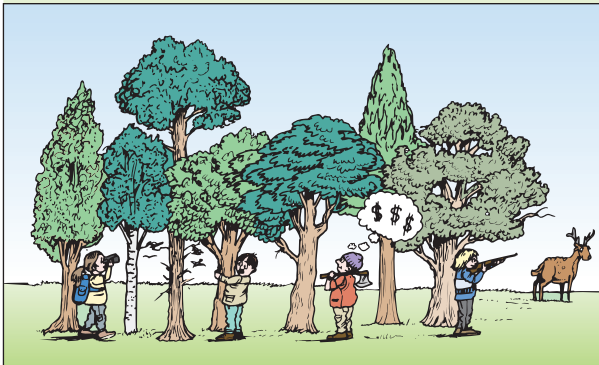
species are enormous; most natural enemies of most pests remain unstudied and often unrecognized. Finally, about 40% of the prescription and non-prescription drugs used throughout the world have active ingredients extracted from plants and animals. Aspirin, probably the world's most widely used drug, was derived originally from the leaves of the tropical willow, *Salix alba*. The nine-banded armadillo (*Dasypus novemcinctus*) has been used to study leprosy and prepare a vaccine for the disease; the Florida manatee (*Trichechus manatus*), an endangered mammal, is being used to help understand hemophilia; while the rose periwinkle (*Catharanthus roseus*), a plant from Madagascar, has yielded two potent drugs effective in treating blood cancer. In all these cases, the species can be thought of as representing *provisioning ecosystem services* (see Section 13.1.2).

Other species have indirect economic value. For example, many wild insects are responsible for pollinating crop plants. This is another provisioning service. In a different context, the monetary value of ecotourism, which depends on biodiversity, is becoming ever more considerable. Each year, nearly 200 million adults and children in the USA take part in nature recreation and spend about \$4 billion on fees, travel, lodging, food and equipment. Moreover, ecotourists, who visit a country wholly or partly to experience its biological diversity, spend approximately \$12 billion a year worldwide on their enjoyment of the natural world (Primack, 1993). On a smaller scale, a multitude of natural history films, books and educational programs are 'consumed' annually without harming the wildlife upon which they are based. In these

contexts, biodiversity provides *cultural ecosystem services*. More ingenuity is required to find ways to measure the indirect economic benefits that accrue as a result of natural biodiversity; for example, biological communities can be of vital importance by maintaining the chemical quality of natural waters, in buffering ecosystems against floods and droughts, in protecting and maintaining soils, in regulating local and even global climate, and in breaking down or immobilizing organic and inorganic wastes. All of these are *regulating ecosystem services*.

It should be noted that many people point to ethical grounds for conservation, with every species being of value in its own right – a value that would still exist even if people were not here to appreciate or exploit them. From this perspective even species with no conceivable economic value require protection.

It would be wrong, though, to see things only from the point of view of conservation – not that there are really arguments *against* conservation as such, but there are arguments in favor of the human activities that make conservation a necessity: agriculture, the felling of trees, the harvesting of wild animal populations, the exploitation of minerals, the burning of fossil fuels, irrigation, the discharge of wastes and so on. To be effective, it is likely that the arguments of conservationists must ultimately be framed in cost–benefit terms because governments will always determine their policies against a background of the money they have to spend and the priorities accepted by their electorates.



*A government conservation authority is considering a proposal to designate a marine reserve at a rocky promontory of great scenic beauty. The site is very diverse in species, including a few that are rare. Commercial and recreational fishers wish to continue fishing at this unusually productive site, local people have mixed feelings about an expected influx of tourists, while conservationists (who mostly live a long way from the site) believe that the conservation value is such that no fishing should be permitted and visitor numbers should be strictly controlled. Imagine that you are an arbitrator chairing a meeting of all interested parties. What arguments do you think they will put forward? What decision would you reach and why?*



Conservation biology relies on an understanding of the threats facing biodiversity (Section 14.2). After presenting this background, we consider in Section 14.3 the options open to conservation biologists to maintain or restore biodiversity. Then, in Section 14.4 we consider some of the issues confronting conservation biologists in the face of global climate change. Section 14.5 provides the final word.

## 14.2 Threats to biodiversity

A basic aim of conservation is to prevent species from becoming extinct either regionally or globally. But how do we define the risk of extinction that a species faces? A species can be described as:

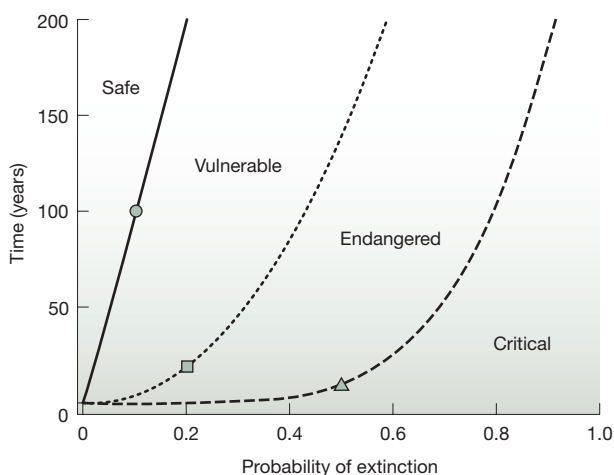
- *critically endangered* if there is considered to be more than a 50% probability of extinction in 10 years or three generations, whichever is longer (Figure 14.2);
- *endangered* if there is more than a 20% chance of extinction in 20 years or five generations;
- *vulnerable* if there is a greater than 10% chance of extinction in 100 years;
- *near threatened* if a species is close to qualifying for a threat category or judged likely to qualify in the near future;
- of *least concern* if a species does not meet any of these threat categories (Rodrigues et al., 2006).

Based on the above criteria, for example, 12% of bird species, 20% of mammals and 32% of amphibians are threatened with extinction (being critically endangered, endangered or vulnerable; Rodrigues et al., 2006).

Species that are at high risk of extinction are almost always rare, but not all rare species are at risk. We need to ask what precisely we mean by rare. A species may be rare in the sense that its geographic range is small, or in the sense that its habitat range is narrow, or because local populations, even where they do occur, are small. Species that are rare on all three counts, such as the giant panda

the classification of threat

there are several ways of being rare



**Figure 14.2**

Levels of threat as a function of time and probability of extinction. The circle represents a 10% probability (i.e. 0.1) of extinction in 100 years (minimum criterion for a population to be designated 'vulnerable'). The square represents a 20% probability of extinction in 20 years (minimum criterion for the designation 'endangered'). The triangle represents a 50% probability of extinction in 10 years (minimum criterion for the designation 'critically endangered').

(*Ailuropoda melanoleuca*), are intrinsically vulnerable to extinction. However, species need only be rare in one sense in order to become endangered. For example, the peregrine falcon (*Falco peregrinus*) is broadly distributed across habitats and geographic regions, yet, because it exists always at low densities, local populations in the USA have become extinct and have had to be re-established with individuals bred in captivity (see Box 13.1).

some species have rarity thrust upon them

Nevertheless, rare species, just by virtue of their rarity, are not necessarily at risk of extinction. In fact it seems that many, probably most, species are naturally rare. We have already said (see Chapter 2) that almost everything is almost always absent from almost everywhere. Succinctly: many species are born rare – but others have rarity thrust upon them. Other things being equal, it will be easier to make a rare species extinct, simply because a localized effect may be sufficient to push it to the brink. Next, therefore, we deal with the various categories of human influence that increase the chances of species extinction.

### 14.2.1 Overexploitation

large animals are prone to overexploitation

The essence of overexploitation is that populations are harvested at a rate that is unsustainable, given their natural rates of mortality and capacities for reproduction (see Section 12.3). We have already discussed the idea that in prehistoric times humans were responsible for the extinction of many large animals, the so-called megaherbivores, by overexploiting them (see Section 10.6). In more recent times, the history of the great whales has followed a similar pattern, while today we are still taking our toll of other vulnerable giants. Sharks provide an interesting example. Among the most feared of species (although attacks are much rarer than held in the popular imagination), large numbers are taken for sport, many others to make shark fin soup, while a large proportion of the estimated annual 200 million shark kills are accidental by-catches of commercial fishing. Evidence is mounting that many species of shark have been declining in abundance, a trend that should come as no surprise given their late ages of maturity, slow reproductive cycles and low fecundities (Cortes, 2002). Sharks are among the most important predators in the marine environment, and their enforced rarity may have widespread repercussions in ocean communities.

the threat posed by collectors

A feature of animals that are collected for ornamentation, whether for their body parts or as exotic pets, is that their value to collectors goes up as they become more rare. Thus, instead of the normal safeguard of a density-dependent reduction in consumption rate at low density (see Section 7.5), the very opposite occurs. The phenomenon is not restricted to animals. New Zealand's endemic mistletoe (*Trilepidia adamsii*), for example, parasitic on a few forest understorey shrubs and small trees, was undoubtedly overcollected to provide herbarium specimens. Always a rare species, its extinction (recorded from 1867 to 1954 but not seen since) was due to overcollecting combined with forest clearance and perhaps an adverse effect on fruit dispersal because of reductions in bird populations.

### 14.2.2 Habitat disruption

Habitats may be adversely affected by human influence in three main ways. First, a proportion of the habitat available to a particular species may simply be destroyed, for urban and industrial development or for the production of food

and other natural resources such as timber. Second, habitat may be degraded by pollution (see Chapter 13) to the extent that conditions become untenable for certain species. Third, habitat may be disturbed by human activities to the detriment of some of its occupants.

Forest clearance has been, and is still, the most pervasive of the forces of habitat destruction. Much of the native temperate forest in the developed world was destroyed long ago, while current rates of deforestation in the tropics are 1% or more per annum. As a consequence, more than half of the wildlife habitat has been destroyed in most of the world's tropical countries. The process of habitat destruction often results in the habitat available to a particular species being more fragmented than was historically the case. This can have several repercussions for the populations concerned, a point we take up again in Section 14.2.4.

Degradation by pollution can take many forms, from the application of pesticides that harm non-target organisms, to acid rain with its adverse effects on organisms as diverse as forest trees, amphibians in ponds and fish in lakes, to global climate change that may turn out to have the most pervasive influence of all. Aquatic environments are particularly vulnerable to pollution. Water, inorganic chemicals and organic matter enter from drainage basins, with which streams, rivers, lakes and continental shelves are intimately connected. Land use changes, waste disposal and water impoundment and abstraction can profoundly affect their patterns of waterflow and the quality of their water (Allan and Flecker, 1993).

Habitat disturbance is not such a pervasive influence as destruction or degradation but certain species are particularly sensitive. For example, diving and snorkeling on coral reefs, even in marine protected areas, can cause damage through direct physical contact with hands, body, equipment and fins. Often the disturbance is minor, but this can amount to cumulative damage and reduction in the populations of vulnerable branching corals. In one analysis of 214 divers in a marine park on Australia's Great Barrier Reef, 15% of divers damaged or broke corals, mostly by fin flicks (Rouphael & Inglis, 2001). Impacts were much more likely to be caused by male than female divers, whilst specialist underwater photographers caused more damage on average (1.6 breaks per 10 minutes) than divers without cameras (0.3 breaks per 10 minutes). Nature recreation, ecotourism and even ecological research are not without risk of disturbance and the decline of the populations concerned.

habitat may be destroyed . . .

. . . or degraded . . .

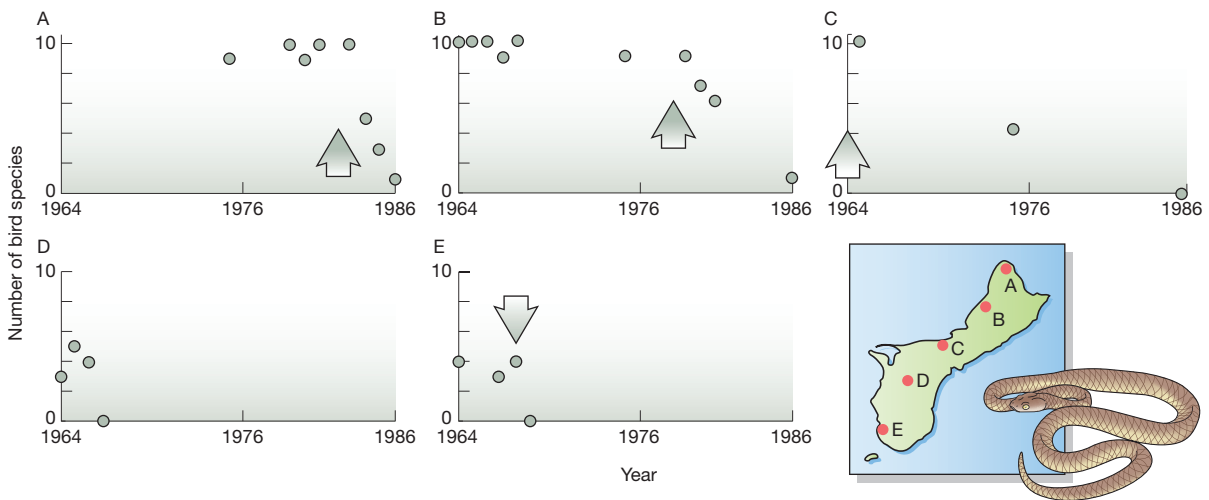
. . . or disturbed

### 14.2.3 Introduced species

Invasions of exotic species into new geographic areas sometimes occur naturally and without human agency. However, human actions have increased this trickle to a flood. Human-caused introductions may occur either accidentally as a consequence of human transport, or intentionally but illegally to serve some private purpose, or legitimately to procure some hoped-for public benefit by bringing a pest under control, producing new agricultural products or providing novel recreational opportunities. Many introduced species are assimilated into communities without much obvious effect. However, some have been responsible for dramatic changes to native species and natural communities.

For example, the accidental introduction of the brown tree snake *Boiga irregularis* onto Guam, an island in the Pacific, has through nest predation reduced

introduced predators



**Figure 14.3**

Decline in the number of forest bird species at five locations on the island of Guam. Large arrows indicate the first sightings of the brown tree snake at each location (in location D, the snake was first sighted in the early 1950s).

10 endemic forest bird species to the point of extinction. The gradual spread of the snake from its bridgehead population in the center of the island has been paralleled by the timing of the loss of bird species to the north and south (Figure 14.3). Similarly, the introduction as a source of human food of the predaceous Nile perch (*Lates nilotica*) to the enormously species-rich Lake Victoria in East Africa has driven most of its 350 endemic species of fish to extinction or near extinction (Kaufman, 1992).

Conservation biologists are particularly concerned about the effects of introduced species wherever there are communities of native organisms that are largely endemic (that is, live nowhere else in the world). Indeed, one of the major reasons for the world's great biodiversity is the occurrence of centers of endemism so that similar habitats in different parts of the world are occupied by different groups of species that happen to have evolved there. If every species naturally had access to everywhere on the globe, we might expect a relatively small number of successful species to become dominant in each biome. The extent to which this homogenization can happen naturally is restricted by the limited powers of dispersal of most species in the face of the physical barriers that exist to dispersal. By virtue of the transport opportunities offered by humans, these barriers have been breached by an ever-increasing number of exotic species. The effects of introductions have been to convert a hugely diverse range of local community compositions into something much more homogeneous.

It would be wrong, however, to conclude that introducing species to a region will inevitably cause a decline in species richness there (Sax & Gaines, 2003). For example, there are numerous species of plants, invertebrates and vertebrates found in continental Europe but absent from the British Isles (many because they have so far failed to recolonize after the last glaciation). Their introduction would be likely to augment British biodiversity. The significant detrimental effect noted above arises where aggressive species provide a novel challenge to endemic biotas ill equipped to deal with them.

introductions leading to  
homogenization

### 14.2.4 Demographic risks associated with small populations

Much of conservation biology is a crisis discipline. Thus, for example, the remaining population of giant pandas in China (or yellow-eyed penguins in New Zealand or spotted owls in North America) has become so small that if nothing is done the species may become extinct within a few years or decades. There is a pressing need to understand the dynamics of small populations.

These are governed by a high level of uncertainty – whereas large populations can be described as being governed by the law of averages (Caughley, 1994). Three kinds of uncertainty or variation are of particular importance to the fate of small populations.

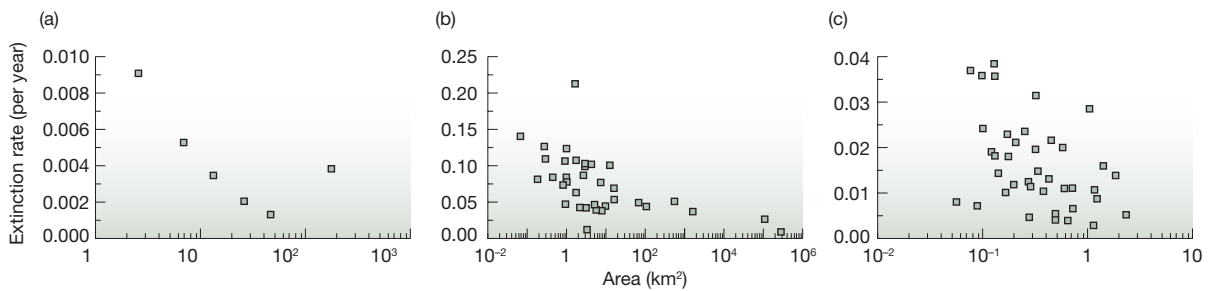
- 1 *Demographic uncertainty.* Random variations in the number of individuals that are born male or female, or in the number that happen to die or reproduce in a given year, or in the genetic ‘quality’ of the individuals in terms of survival/reproductive capacities can matter very much to the fate of small populations. Suppose a breeding pair produces a clutch consisting entirely of females – such an event would go unnoticed in a large population but would be the last straw for a species down to its last pair.
- 2 *Environmental uncertainty.* Unpredictable changes in environmental factors, whether ‘disasters’ (such as floods, storms or droughts of a magnitude that occurs very rarely) or more minor (year to year variation in average temperature or rainfall), can also seal the fate of a small population. A small population is more likely than a large one to be reduced by adverse conditions to zero or to numbers so low that recovery is impossible.
- 3 *Spatial uncertainty.* Many species consist of an assemblage of subpopulations that occur in more or less discrete patches of habitat (habitat fragments). Since the subpopulations are likely to differ in terms of demographic uncertainty, and the patches they occupy in terms of environmental uncertainty, the dynamics of extinction and local recolonization can be expected to have a large influence on the chance of extinction of the overall metapopulation (see Section 9.3).

To illustrate some of these ideas, take the demise in North America of the heath hen (*Tympanuchus cupido cupido*). This bird was once extremely common from Maine to Virginia. Being highly edible and easy to shoot (and also susceptible to introduced cats and affected by conversion of its grassland habitat to farmland), it had by 1830 disappeared from the mainland and was only found on the island of Martha’s Vineyard. In 1908 a reserve was established for the remaining 50 birds and by 1915 the population had increased to several thousand. However, 1916 was a bad year. Fire (a disaster) eliminated much of the breeding ground, there was a particular hard winter coupled with an influx of goshawks (environmental uncertainty) and finally poultry disease arrived on the scene (another disaster). At this point the remnant population was likely to have become subject to demographic uncertainty; for example, of the 13 birds remaining in 1928 only two were females. A single bird was left in 1930 and the species went extinct in 1932.

Of the high risk factors associated with local extinctions of plant and animal species, having a small habitat area is probably the most pervasive. Figure 14.4

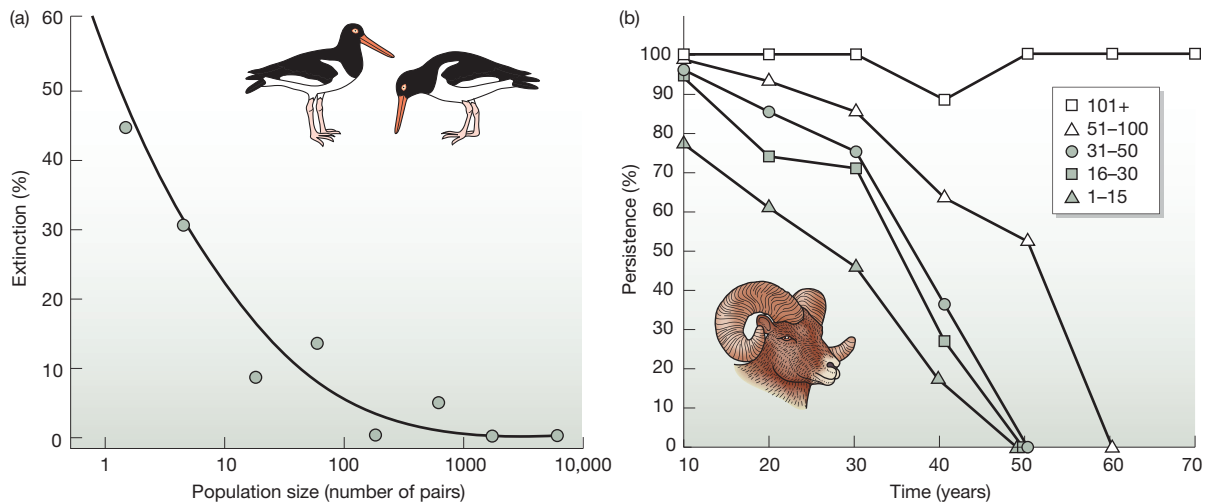
the case of the heath hen

the importance of habitat area



**Figure 14.4**

Percentage extinction rates as a function of habitat area for (a) zooplankton in lakes in northeastern USA, (b) birds on northern European islands, and (c) vascular plants in southern Sweden.



**Figure 14.5**

(a) The extinction rate of island birds is higher for small populations. (b) The percentage of populations of bighorn sheep in North America that persists over a 70-year period is lowest where the initial population size was small (green triangles: 1–15 individuals) and is highest where initial population size was large (open squares: >101 individuals). The regression line in (a) is statistically significant.

shows the negative relationships for a variety of taxa between annual extinction rate and area. No doubt the main reason for the vulnerability of populations in small areas is the fact that the populations themselves are small. This is illustrated in Figure 14.5 for bird species on islands and for bighorn sheep in various desert areas in southwest USA.

#### habitat fragmentation

In fact, loss of habitat frequently results not only in a reduction in the absolute size of a population but also the division of the original population into a meta-population of semi-isolated subpopulations. Further fragmentation can result in a decrease in the average size of fragments, an increase in the distance between them and an increase in the proportion of edge habitat (Burgman et al., 1993). A question of fundamental importance, then, is whether a species is more at risk simply because its population is subdivided. In other words, would a single population of a given size be less or more at risk than one divided into a number of subpopulations in habitat fragments?

The answer lies in the balance between the connectedness of different subpopulations on the one hand, and the correlation between the dynamics of different subpopulations on the other. Thus, where the probability of dispersal between fragments (that is, connectedness) is high, metapopulations will tend to persist for longer than unfragmented populations. The reason is because when individual subpopulations go extinct, there is a good chance that they will be restarted by a colonist from another subpopulation. However, where extinction events in different subpopulations are strongly correlated (because environmental variation acts identically in all fragments), metapopulations will be more at risk than unfragmented populations. This is because the individual subpopulations, being small, are vulnerable to extinction, and when one goes extinct, they all tend to.

So far, attention has been focused on individual species, treating them as though they were largely independent entities and applying what we know about population dynamics. However, it hardly needs to be pointed out that conservation of biodiversity also requires a broader perspective in which we apply our knowledge of whole communities. If we ignore community interactions, a chain of extinctions may follow inexorably from the extinction of a particular native species, which therefore deserves special attention. Flying foxes in the genus *Pteropus*, which occur on South Pacific islands, are the major, and sometimes the only, pollinators and seed dispersers for hundreds of native plants (many of which are of considerable economic importance, providing medicines, fiber, dyes, prized timber and foods). Flying foxes are highly vulnerable to human hunters and there is widespread concern about declining numbers. On the island of Guam, for example, the two indigenous flying fox species are either extinct, or virtually so, and there are already indications of reductions in fruiting and dispersal (Cox et al., 1991).

chains of extinctions – taking a community perspective

### 14.2.5 Possible genetic problems in small populations

Theory tells conservation biologists to beware genetic problems in small populations that may arise through loss of genetic variation (Box 14.2). The preservation of genetic diversity is important in the first place because of the long-term evolutionary potential it provides. Rare forms of a gene (alleles), or combinations of alleles, may confer no immediate advantage but could turn out to be well suited to changed environmental conditions in the future. Small populations tend to have less variation and hence lower evolutionary potential.

loss of evolutionary potential

A more immediate potential problem is inbreeding depression. When populations are small there is a tendency for related individuals to breed with one another. All populations carry recessive alleles that can be lethal to individuals when homozygous (i.e. when the alleles provided by the mother and father are identical). Individuals that breed with close relatives are more likely to produce offspring where the harmful alleles are derived from both parents – so the deleterious effect is expressed. There are many examples of inbreeding depression – breeders of domesticated animals and plants, for example, have long been aware of reductions in fertility, survivorship, growth rates and resistance to disease.

the risk of inbreeding depression

In their study of 23 local populations of the rare plant *Gentianella germanica* in grasslands in the Jura Mountains (Swiss–German border), Fischer and Matthies (1998) found a negative correlation between reproductive performance and





## 14.2 Quantitative aspects

### 14.2 QUANTITATIVE ASPECTS

#### What determines genetic variation?

Genetic variation is determined primarily by the joint action of natural selection and genetic drift (where the frequency of genes in a population is determined by chance rather than evolutionary advantage). The relative importance of genetic drift is higher in small isolated populations that, as a consequence, are expected to lose genetic variation. The rate at which this happens depends on the effective population size ( $N_e$ ). This is the size of the 'genetically idealized' population to which the actual population ( $N$ ) is equivalent in genetic terms.

$N_e$  is usually less, often much less, than  $N$ , for a number of reasons [detailed formulae can be found in Lande and Barrowclough (1987)]:

- 1 If the sex ratio is not 1:1; for instance, with 100 breeding males and 400 breeding females,  $N = 500$  but  $N_e = 320$ .
- 2 If the distribution of progeny from individual to individual is not random; for instance, if 500 individuals each produce one individual for the next generation on average ( $N = 500$ ), but the variance in progeny production is five (with random variation this would be one), then  $N_e = 100$ .
- 3 If population size varies from generation to generation, then  $N_e$  is disproportionately

influenced by the smaller sizes; for instance, for the sequence 500, 100, 200, 900, 800, mean  $N = 500$  but  $N_e = 258$ .

How many individuals are needed to maintain genetic variability? Franklin and Frankham (1998) suggest that an effective population size of 500–1000 might be needed to maintain longer term evolutionary potential.

Greater prairie chickens (*Tympanuchus cupido pinnatus*), closely related to the heath hens in Section 14.2.4, provide a good example of how genetic diversity may be related to population size. These birds were once widespread throughout the prairies of North America, but with the loss and fragmentation of this habitat many populations have become small and isolated. Johnson et al. (2003) used molecular biology techniques (see Section 8.2) to measure genetic diversity in both large (from 1000 to more than 100,000 individuals) and small prairie chicken populations (fewer than 1000 individuals). The mean number of alleles (per gene) ranged from 7.7 to 10.3 in the large populations, but was only 5.1–7.0 in the small populations. Prairie chicken populations were once linked by the 'gene flow' provided by migrants, keeping genetic diversity high. But current populations are isolated in their habitat fragments.

population size (Figure 14.6a–c). Furthermore, population size decreased between 1993 and 1995 in most of the studied populations, but population size decreased more rapidly in the smaller populations (Figure 14.6d). Seeds taken from small populations produced fewer flowers than seeds from large populations grown under identical conditions. We can conclude that genetic effects are of importance for population persistence in this rare species.

#### 14.2.6 A review of risks

We have seen that extinction may be caused by one of a number of 'drivers', including overexploitation, habitat disruption and introduced species. The relative importance of different drivers for global bird biodiversity is illustrated in

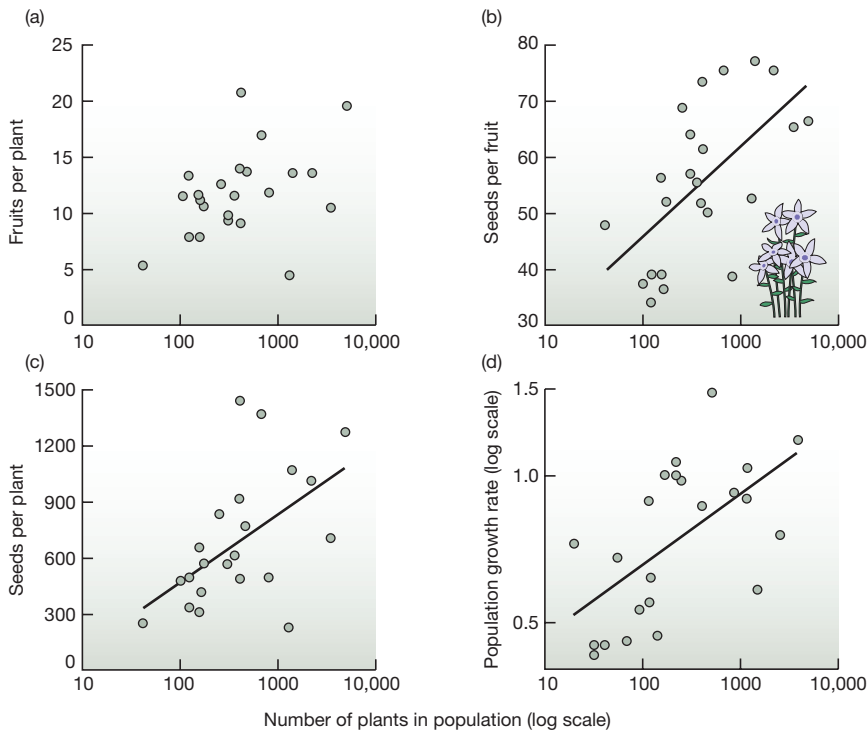


Figure 14.6

Relationships for 23 populations of *Gentianella germanica* between population size and (a) mean number of fruits per plant, (b) mean number of seeds per fruit and (c) mean number of seeds per plant. (d) The relationship between population growth rate from 1993 to 1995 (ratio of population sizes) and population size (in 1994). All regression lines are significant at  $P < 0.05$ ; no line is shown in (a) because the regression is not significant.

Figure 14.7. Bird extinctions during the last five centuries can be attributed, in roughly equal measure, to the effects of invasive species, overexploitation by hunters and habitat loss. Currently, habitat loss is the biggest problem facing threatened species (whether critically endangered, endangered or vulnerable).

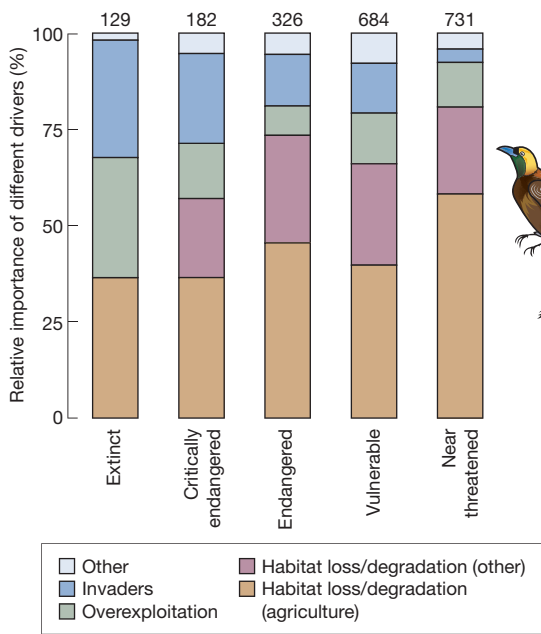
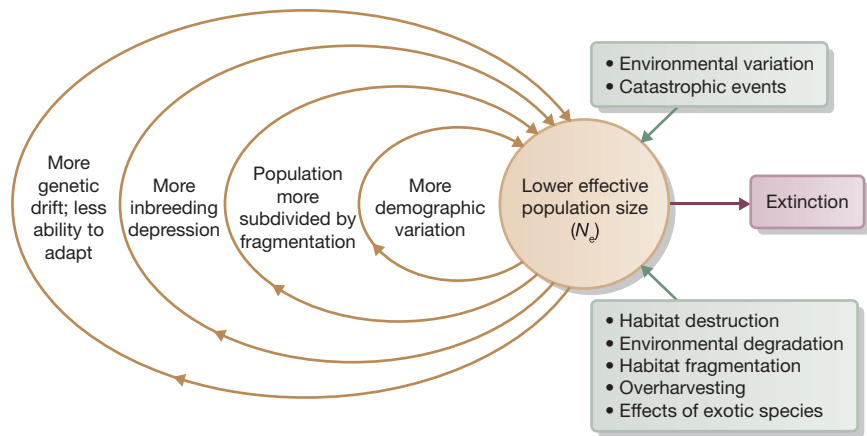


Figure 14.7

Relative importance of different 'drivers' responsible for the loss or endangerment of bird biodiversity. Patterns are shown for five categories of extinction threat (see Section 14.2). The values above each histogram are the numbers of species in each threat category globally. Habitat loss/degradation poses a much bigger risk now than in the past (compare histograms for endangered and vulnerable categories with extinct birds) and this is set to increase in the future, in particular via agricultural expansion (histogram for near threatened species).

### Figure 14.8

Extinction vortices may progressively lower population sizes leading inexorably to extinction.



FROM PRIMACK, 1993

extinction vortices

And in the case of ‘near threatened’ bird species, the ones that managers will have to attend to in future, habitat loss to agriculture is expected to be by far the most important driver.

Some species are at risk for a single reason, but often, as in the case of the New Zealand mistletoe discussed earlier, a combination of factors is at work. It is interesting that no example of extinction due to genetic problems has so far come to light. Perhaps inbreeding depression has occurred, though undetected, as part of the ‘death rattle’ of some dying populations (Caughley, 1994). Thus, a population may have been reduced to a very small size by one or more of the processes described above, and this may have led to an increased frequency of matings among relatives and the expression of deleterious recessive alleles in offspring, leading to reduced survivorship and fecundity and causing the population to become smaller still – the so-called *extinction vortex* (Figure 14.8). The small populations of *Gentianella germanica* (Figure 14.6) may have entered an extinction vortex.

## 14.3 Conservation in practice

Given the environmental circumstances and species characteristics of a particular rare species, what is the chance it will go extinct in a specified period? Alternatively, how big must its population be to reduce the chance of extinction to an acceptable level? These are frequently the crunch questions in conservation biology and a tool, known as *population viability analysis*, is frequently called upon (Section 14.3.1). As a result of population modeling, managers determine the course of action most likely to prevent extinction. Sometimes, however, populations have become so small that their only chance of persistence involves translocation of individuals from viable populations elsewhere or from captive rearing programs. In these cases, managers can call on genetic theory to determine the best individuals to found or augment a population (Section 14.3.2). Conservation action often involves setting aside protected areas, sometimes designed for particular species (to provide a large enough area to accommodate the minimum viable population size) but often to protect biodiversity more generally. We discuss some of the principles of reserve design in Section 14.3.3.

### 14.3.1 Population viability analysis

Data sets such as those for bighorn sheep in desert areas in Figure 14.5b are unusual because they depend on a long-term commitment (in this case, by hunting organizations) to monitor a number of populations. If we set an arbitrary definition of the necessary *minimum viable population* (MVP) as one that will give at least a 95% probability of persistence for 100 years, we can explore data like these to provide an approximate estimate of MVP. Bighorn populations of fewer than 50 individuals all went extinct within 50 years, while only 50% of populations of 51–100 sheep lasted for 50 years. Evidently, for an MVP here we require more than 100 individuals; indeed, for these sheep such populations demonstrated close to 100% persistence over the maximum period studied of 70 years. The value for conservation of studies like this, however, is limited because they deal with species that are generally not at risk.

Simulation models known as *population viability analyses* (PVAs) provide an alternative, more specific way of gauging viability. Usually, these encapsulate survivorships and reproductive rates in age-structured populations (see Chapter 5). Random variations in these elements or in carrying capacity (*K*) can be employed to represent the impact of environmental variation, including that of disasters of specified frequency and intensity. Density dependence can be introduced where required. In the more sophisticated models, every individual is treated separately in terms of the probability, with its imposed uncertainty, that it will survive or produce a certain number of offspring in the current time period. The program is run many times, each giving a different population trajectory because of the random elements involved. The outputs, for each set of model parameters used, include estimates of population size each year and the probability of extinction during the modeled period (the proportion of simulated populations that go extinct).

Koalas (*Phascolarctos cinereus*) are regarded as ‘near threatened’ in Australia, with populations in different parts of the country varying from secure to vulnerable or extinct. Penn et al. (2000) used a widely available PVA tool (known as VORTEX; Lacy, 1993) to model two populations in Queensland, one thought to be declining (Oakey), the other secure (Springsure). Koala breeding commences at 2 years in females and 3 years in males. The other demographic values were derived from extensive knowledge of the two populations and are shown in Table 14.1. Note how the Oakey population had somewhat higher female mortality and fewer females producing young each year. The Oakey population was modeled from 1971 and the Springsure population from 1976 (when first estimates of density were available) and the model trajectories were indeed declining and stable, respectively (Figure 14.9). Over the modeled period, the probability of extinction of the Oakey population was 0.380 (i.e. 380 out of 1000 iterations went extinct) while that for Springsure was 0.063. Managers concerned with critically endangered species do not usually have the luxury of monitoring populations to check the accuracy of their predictions. In contrast, Penn et al. (2000) were able to compare the predictions of their PVAs with real population trajectories, because the koala populations have been continuously monitored since the 1970s (Figure 14.9). The predicted trajectories were close to the actual population trends, particularly for the Oakey population, and this gives added confidence to the modeling approach. The predictive accuracy of VORTEX and other simulation modeling tools has also been shown to be good for 21 other long-term animal data sets (Brook et al., 2000).

trying to determine the minimum viable population

simulation modeling – population viability analysis

koalas – identifying populations at particular risk

Table 14.1

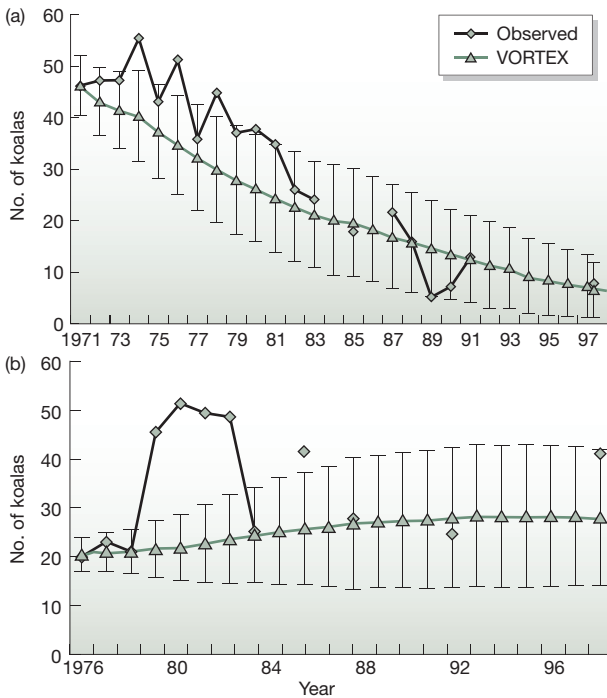
Values used as inputs for simulations of koala populations at Oakey (declining) and Springsure (secure). Values in brackets are standard deviations due to environmental variation; the model procedure involves the selection of values at random from the range. Catastrophes are assumed to occur with a certain probability; in years when the model 'selects' a catastrophe, reproduction and survival are reduced by the multipliers shown (e.g. in a year with a catastrophe, reproduction is reduced to 55% of what it would otherwise have been).

VARIABLE	OAKEY	SPRINGSURE
Maximum age	12	12
Sex ratio (proportion male)	0.575	0.533
Litter size of 0 (%)	57.00 (±17.85)	31.00 (±15.61)
Litter size of 1 (%)	43.00 (±17.85)	69.00 (±15.61)
Female mortality at age 0	32.50 (±3.25)	30.00 (±3.00)
Female mortality at age 1	17.27 (±1.73)	15.94 (±1.59)
Adult female mortality	9.17 (±0.92)	8.47 (±0.85)
Male mortality at age 0	20.00 (±2.00)	20.00 (±2.00)
Male mortality at age 1	22.96 (±2.30)	22.96 (±2.30)
Male mortality at age 2	22.96 (±2.30)	22.96 (±2.30)
Adult male mortality	26.36 (±2.64)	26.36 (±2.64)
Probability of catastrophe	0.05	0.05
Multiplier, for reproduction	0.55	0.55
Multiplier for survival	0.63	0.63
% males in breeding pool	50	50
Initial population size	46	20
Carrying capacity, <i>K</i>	70 (±7)	60 (±6)

AFTER PEW ET AL., 2000

Figure 14.9

Observed koala population trends (diamonds) compared with predicted population performance (triangles, ± 1 SD) based on 1000 repeats of the VORTEX modeling procedure at (a) Oakey and (b) Springsure. Real population censuses were not performed every year.



AFTER PEW ET AL., 2000

How can such modeling be put to management use? Local governments in New South Wales are obliged both to prepare comprehensive koala management plans and to ensure that developers survey for potential koala habitat when a building application affects an area greater than 1 ha. Penn et al. (2000) argue that PVA modeling can be used to determine whether any effort made to protect habitat is likely to be rewarded by a viable population.

The life histories of plants present particular challenges for simulation modeling, including seed dormancy, highly periodic recruitment of seedlings and clonal growth (Menges, 2000). However, as with endangered animals, different management scenarios can be simulated in PVAs. The royal catchfly, *Silene regia*, is a long-lived prairie perennial whose range has shrunk dramatically. Menges and Dolan (1998) collected demographic data for up to 7 years from 16 populations in the US Midwest. The populations, whose total adult numbers ranged from 45 to 1302, had been subject to different management regimes. This species, whose seeds do not show dormancy, has high survivorship and frequent flowering, but successful germination is very episodic – most populations in most years fail to produce seedlings.

Simulation modeling made use of *population projection matrices*, which are particularly useful for analyzing species with overlapping generations. A population projection matrix acknowledges that most life cycles comprise a sequence of distinct classes with different rates of fecundity and survival. A matrix for one of the populations of *S. regia* is illustrated in Table 14.2. Such matrices were produced for each population in each year. Multiple simulations, each lasting 1000 years, were then run for every matrix to determine both the probability of extinction and the population’s finite rate of increase,  $\lambda$ . This term has not yet been introduced, but note that it is related to the population’s intrinsic rate of increase,  $r$ , discussed in Box 5.4. In fact,  $r = \ln \lambda$ . For now, all you need to appreciate is that a population will grow in size when  $\lambda > 1$  and will decline when  $\lambda < 1$ ; a value of  $\lambda = 2$ , for example, means that on average every individual in the population will give rise to two individuals in the next generation (either by producing one surviving offspring and staying alive itself, or by dying but producing two surviving offspring).

Figure 14.10 shows the median population growth rate  $\lambda$  for the 16 populations, grouped into cases where particular management regimes were in place.

the royal catchfly – management of an endangered plant

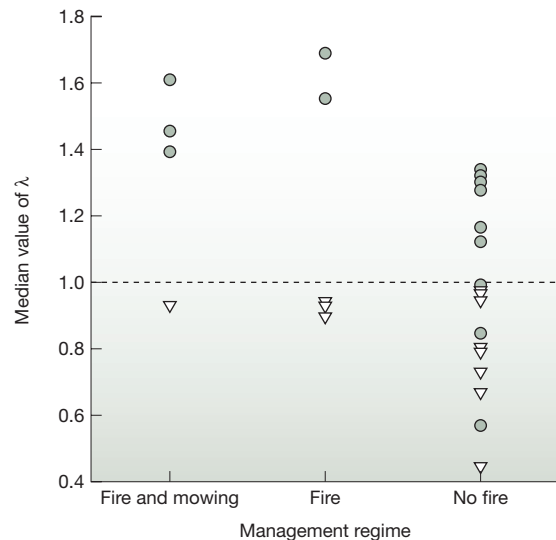
Table 14.2

An example of a projection matrix (using the simulation modeling tool called RAMAS-STAGE) for a particular *Silene regia* population from 1990 to 1991, assuming successful germination of seedlings. The numbers represent the proportion changing from the stage in the column to the stage in the row (bold values represent plants remaining in the same stage). ‘Alive undefined’ represents individuals with no size or flowering data, usually as a result of mowing or herbivory. The numbers in the top row are seedlings produced by flowering plants. The finite rate of increase,  $\lambda$ , for this population is 1.67. (Note that a population will increase when  $\lambda > 1$ , and decrease when  $\lambda < 1$ .) The site is managed by regular burning.

	SEEDLING	VEGETATIVE	SMALL FLOWERING	MEDIUM FLOWERING	LARGE FLOWERING	ALIVE UNDEFINED
Seedling	–	–	5.32	12.74	30.88	–
Vegetative	0.308	<b>0.111</b>	0	0	0	0
Small flowering	0	0.566	<b>0.506</b>	0.137	0.167	0.367
Medium flowering	0	0.111	0.210	<b>0.608</b>	0.167	0.300
Large flowering	0	0	0.012	0.039	<b>0.667</b>	0.167
Alive undefined	0	0.222	0.198	0.196	0	<b>0.133</b>

**Figure 14.10**

Median rates of population increase ( $\lambda$ ) of *Silene regia* populations in relation to management regime, for years with seedling recruitment (shaded circles) and without (open triangles). Unburned management regimes include just mowing, herbicide use or no management. All sites above the dashed line have values for  $\lambda$  of  $>1.0$ , indicating their capacity to grow in size. Those below the line are on paths to extinction.



AFTER MENGES &amp; DOLAN, 1998

This was done both for years when recruitment of seedlings occurred and for years when seedling recruitment did not occur. All sites where  $\lambda$  was greater than 1.35 when recruitment took place are managed by burning and some by mowing as well; none of these were predicted to go extinct during the modeled period. On the other hand, populations with no management regime, or whose management does not include fire, had lower values for  $\lambda$  and all except two had predicted extinction probabilities (over 1000 years) of from 0.10 to 1.00.

The obvious management recommendation is to use prescribed burning to provide opportunities for seedling recruitment. Low establishment rates of seedlings may be due to rodents or ants eating fruits or to competition for light with other plants – burnt areas probably reduce one or both of these negative effects.

### 14.3.2 Dealing with genetic issues

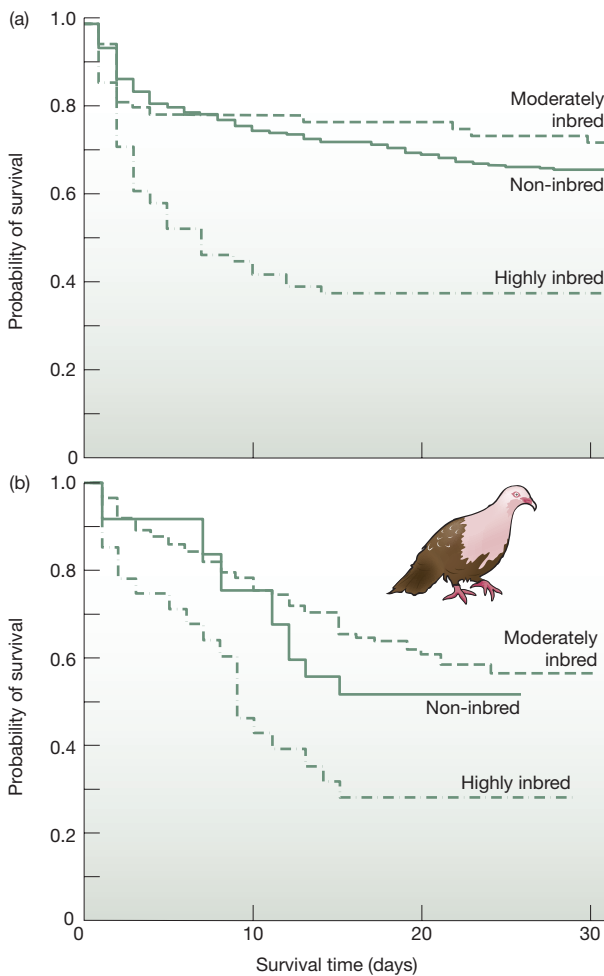
#### recovery of the pink pigeon

The pink pigeon (*Columba mayeri*), once widespread on the island of Mauritius, was down to only nine or 10 birds in 1990. As a result of the release of captive-bred individuals the population had swelled to 355 free-living individuals (plus more in captivity) by 2003. In captivity, the aim was to manage matings to retain high levels of genetic diversity and to minimize inbreeding. The captive population was originally descended from just 11 founder individuals, augmented in 1989–1994 by adding 12 more founder individuals (offspring of the remaining wild individuals).

Once captive-reared birds are released into the wild the incidence of inbreeding depression is not easy to control – the tactic of releasing a large number of birds provides the greatest chance of success. Between 1987 and 1997, 256 birds were reintroduced on Mauritius – wherever possible selecting birds with minimal inbreeding (based on records in breeding ‘stud books’) and releasing them in groups with good representation of the different founder ancestries. All birds were banded for unique identification.

The genetics and ecological success of both captive and wild populations have been carefully monitored. Thus, we can evaluate the impact of inbreeding



**Figure 14.11**

Effect of inbreeding on probability of survival to 30 days of age of pink pigeon nestlings (a) in captivity and (b) in the wild population. Inbreeding is expressed as an index derived from known ancestry in relation to 23 founder individuals. The fewer founders in a bird's ancestry, the higher the index of inbreeding. Birds are grouped into three classes – non-inbred, moderately inbred and highly inbred. Only highly inbred birds show a powerful effect of inbreeding.

AFTER SWINNERTON ET AL., 2004

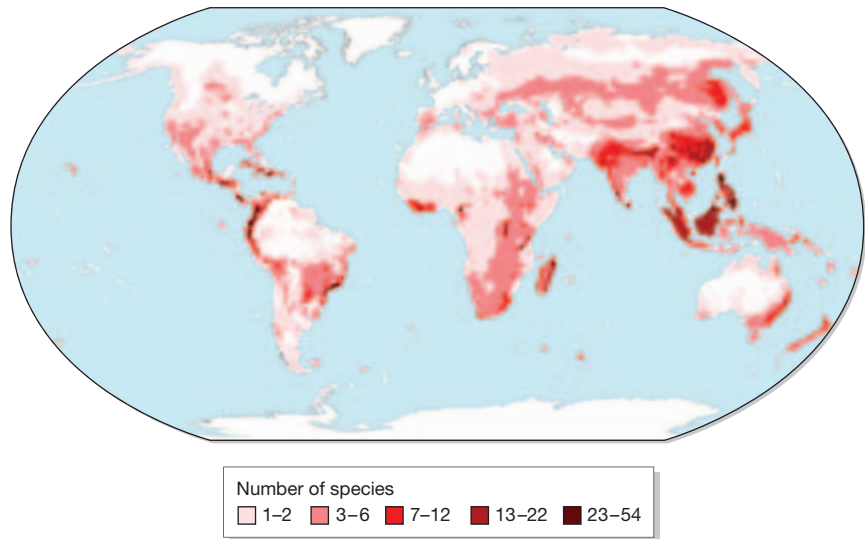
on survival and reproduction under the controlled situation of captive rearing and also in the more risky circumstances of the wild. Inbreeding reduced egg fertility and survival of nestlings (Figure 14.11), but effects were only strongly marked in the most inbred birds. The pink pigeon reintroduction success story has the added benefit of providing a rare quantification of the value of avoiding inbreeding when managing endangered populations.

### 14.3.3 Selecting conservation areas

Producing survival plans for individual species may be the best way to deal with species recognized to be in deep trouble and identified to be of special importance (e.g. keystone species described in Section 9.5.2, evolutionarily unique species or charismatic large animals that are easy to 'sell' to the public). However, there is no possibility that all endangered species could be dealt with one at a time. Conservation dollars are simply too limited for this. We can, though, expect to conserve the greatest biodiversity if we protect whole communities by setting aside protected areas. In fact, protected areas of various kinds (national parks,

**Figure 14.12**

Distribution of biodiversity hotspots, showing numbers of species of globally threatened birds plus amphibians mapped on an equal area basis (each grid cell is 3113 km<sup>2</sup>).



AFTER RODRIGUES ET AL., 2006

biodiversity hotspots

the design of nature reserves

nature reserves, sites of special scientific interest, etc.) grew both in number and area during the 20th century. Currently, about 7.9% of the world's land area is protected (and 0.5% of the sea area; Balmford et al., 2002).

It is important to devise priorities so that the restricted number of new protected areas, in terrestrial and marine settings, can be evaluated systematically and chosen with care. We know that the biotas of different locations vary in species richness (with particular centers of diversity), the extent to which the biota is unique (with centers of endemism) and the extent to which the biota is endangered (with hotspots of extinction, for example because of imminent habitat destruction). One or more of these criteria could be used to prioritize potential areas for protection (Figure 14.12).

A perhaps rather surprising application of island biogeography theory (see Section 10.5.1) is in nature conservation. This is because many conserved areas and nature reserves are surrounded by an 'ocean' of habitat made unsuitable, and therefore hostile, by people. Can the study of islands in general provide us with design principles that can be used in the planning of nature reserves? The answer is a cautious 'Yes'; some general points can be made.

- 1 One problem that conservation managers sometimes face is whether to construct one large reserve or several small ones adding up to the same total area. If the region is homogeneous in terms of conditions and resources, it is quite likely that smaller areas will contain a subset of the species present in a larger area. In such a case it would be preferable to construct the larger reserve in the expectation of conserving more species in total (this recommendation derives from the species–area relationships discussed in Section 10.5.1).
- 2 On the other hand, if the region as a whole is heterogeneous, then each of the small reserves may support a different group of species and the total conserved might exceed that in one large reserve of the same size. In fact, collections of small islands tend to contain more species than a comparable area composed of one or a few large islands. The pattern

is similar for habitat islands and, most significantly, for national parks. Thus, several small parks contained more species than larger ones of the same area in studies of mammals and birds in East African parks, of mammals and lizards in Australian reserves, and of large mammals in national parks in the USA. It seems likely that habitat heterogeneity is a general feature of considerable importance in determining species richness.

- 3 A point of particular significance is that local extinctions are common events, and so recolonization of habitat fragments is critical for the survival of fragmented populations. Thus, we need to pay particular attention to the spatial relationships amongst fragments, including the provision of dispersal corridors. There are potential disadvantages – for example, corridors could increase the correlation among fragments of catastrophic effects, such as the spread of fire or disease – but the arguments in favor are persuasive. Indeed, high recolonization rates (even if this means conservation managers themselves moving organisms around) may be indispensable to the success of conservation of endangered metapopulations. Note especially that human fragmentation of the landscape, producing subpopulations that are more and more isolated, is likely to have had the strongest effect on populations with naturally low rates of dispersal. Thus, the widespread declines of the world's amphibians may be due, at least in part, to their poor potential for dispersal (Blaustein et al., 1994).

The basic approach in *complementarity* selection is to proceed in a stepwise fashion, selecting at each step the site that is most *complementary* to those already selected in terms of the biodiversity it contains. In the case of the coastal marine fishes around Western Australia, the results of a complementarity analysis showed that more than 95% of the total of 1855 species could be represented in just six, appropriately located, sections (each 100 km long) (see stars in Figure 14.13).

principles for selecting new reserves: 'complementarity' . . .

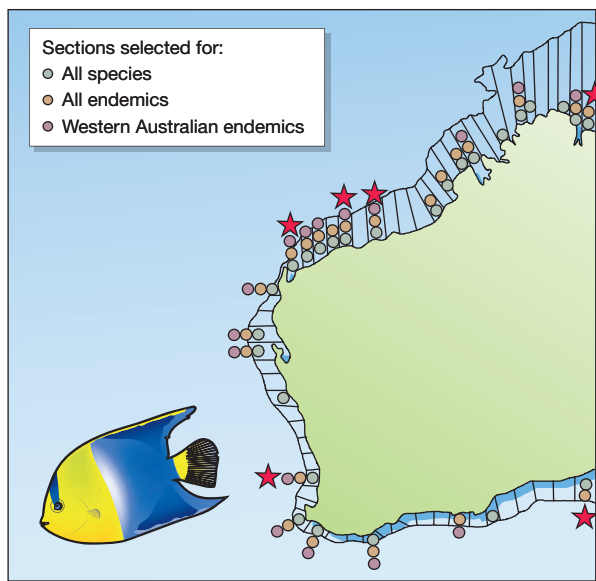
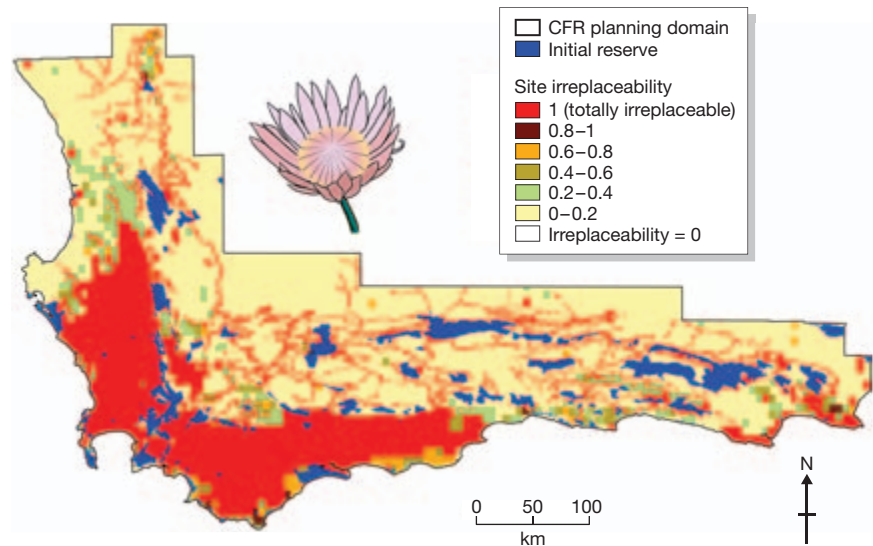


Figure 14.13

Coastline of Western Australia divided into 100 km lengths and showing the results of complementarity analysis to identify the minimum number of sites needed to include all the fish biodiversity for the region. Analyses were performed using all fish species, and separately for species endemic to Australia (found nowhere else) or those endemic to Western Australia. In the case of total fish biodiversity, 26 areas were needed if all 1855 fish species were to be incorporated (green circles) but only 6 areas (stars) would be needed to incorporate more than 95% of the total.

**Figure 14.14**

Map of South Africa's Cape Floristic Region (CFR) showing site irreplaceability values for achieving a range of conservation targets in the 20-year conservation plan for the region. Irreplaceability is a measure, varying from 0 to 1, which indicates the relative importance of an area for the achievement of regional conservation targets. Existing reserves are shown in blue.



... or 'irreplaceability'

An approach that contrasts subtly with complementarity analysis concerns the *irreplaceability* of each potential area. Irreplaceability is defined as the likelihood of an area being required to achieve conservation targets or, conversely, the likelihood of one or more targets not being achieved if the area is not included. Cowling et al. (2003) used irreplaceability analysis as part of their conservation plan for South Africa's Cape Floristic Province – a global hotspot with more than 9000 plant species. The research team identified a variety of conservation targets including, among others, the minimum acceptable number of species of *Protea* plants to be safeguarded (for which the region is famous), the minimum permissible number of ecosystem types and even the minimum permissible number of individuals (or populations) of large mammal species. They used an irreplaceability approach to guide the choice of areas to add to existing reserves that would best achieve the conservation targets (Figure 14.14). The ambitious aim is to achieve their overall goal by 2020 and they conclude that, in addition to areas that already have statutory protection, 42% of the Cape Floristic Province, comprising some 40,000 km<sup>2</sup>, will need some level of protection. This includes all cases of high irreplaceability (>0.8) and some areas that are unimportant in terms of *Protea* and ecosystem types but are needed to provide for the needs of large mammals in lowland areas.

## 14.4 Conservation in a changing world

As we have seen, a basic idea that derives from island biogeography theory is that smaller areas contain fewer species. One way to assess the extinction risk of endemic species under global climate change is to estimate, on the basis of predicted changes to temperature and rainfall, the loss in area of key habitats. Thus, for example, the characteristic biota of the Cape Floristic Province, discussed in Section 14.3.3, is expected to lose 65% of its habitable area by 2050. On the basis of the general pattern relating species richness to area, this represents a reduction of 24% in number of species (Thomas et al., 2004). Moreover, this conclusion is based on the optimistic assumption that all *Protea* species are capable of dispersing to all

currently uninhabited areas that become inhabitable (global climate change will also make some uninhabitable areas more hospitable). If no dispersal is assumed, and future ranges are simply those reduced parts of current ranges that remain inhabitable, 30–40% of species seem at risk of extinction. Similar fates could await diverse animal and plant taxa around the world (Box 14.3). In many cases, though, a suitable choice of protected areas can minimize the predicted losses.



## 14.3 Topical EConcerns

### 14.3 TOPICAL EConcerns

The following article appeared in the *Boston Globe* on January 2, 2007.

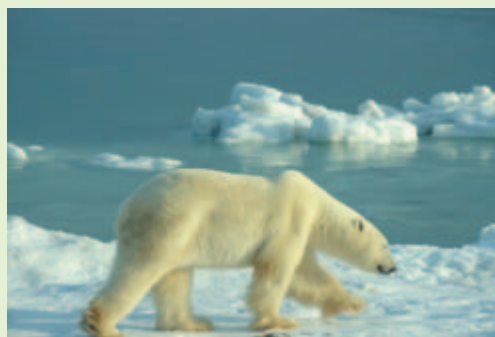
#### The silence of the polar bears

Arctic polar bears are becoming canaries in the mine, warning of the consequences of global warming.

Even the Bush administration has been forced, grudgingly, to acknowledge this. Last week, it proposed to put the bears on the threatened species list because rising temperatures in the Arctic are depriving them of the ice platforms from which they hunt seals. But Interior Secretary Dirk Kempthorne acted only under pressure of a suit from environmental organizations, and has refused to admit that greenhouse gas emissions from vehicles and smokestacks are causing the ice loss and would have to be cut back to save the bears' habitat.

The administration still has a long way to go before it comes out of the denial that has left it on the sidelines as other nations take action to reduce greenhouse gases. If the United States does not quickly take a leadership role on this issue, polar bears will be only one of many species to suffer. So will human beings.

It is no surprise that one of the first species to be so affected by climate change is in the Arctic. In northern latitudes, temperatures are rising at twice the global rate and could rise by an additional 13 degrees Fahrenheit by the end of the century. Researchers say summer sea ice will decline by 50 to 100 percent, with a worst-case scenario from the National Center



© FLP 10140-00336-140

for Atmospheric Research predicting the ice could be all gone by 2040.

In areas where scientists have studied many of the world's 20,000 to 25,000 polar bears, they report thinner animals with lower female reproductive rates and lower survival rates for cubs. Bears have been seen cannibalizing one another and have drowned during ever-longer swims from ice floe to ice floe.

(Copyright 2007 Globe Newspaper Company; reprinted by permission.)

*The proposal to declare polar bears 'threatened' was just the start of a year-long process in which the Department of Interior was due to call for comments before taking final action. The Department is also supposed to be working out a plan for the recovery of polar bears by limiting factors that harm them. What components would you expect to be included in a management plan? Do you think any plan can be effective unless it calls for measures to reduce emissions of carbon dioxide?*

ensuring that nature reserves  
are in the right places

Temperature and rainfall also strongly influence the life cycle of butterflies. Beaumont and Hughes (2002) used predicted climate changes to model the future distributions of 24 Australian butterfly species. Under even a moderate set of future conditions (temperature increase of 0.8–1.4°C by 2050) the distributions of 13 of the species decreased by more than 20%. Most at risk are butterflies, such as *Hypochrysops halyetus*, that not only have specialized food plant requirements but also depend on the presence of ants for a mutualistic relationship (see Section 8.4) – this species is predicted to lose 58–99% of its current climatic range. Moreover, only one-fourth of its predicted future distribution occurs in locations that it currently occupies. This result highlights a general point for managers: regional conservation efforts and current nature reserves may turn out to be in the wrong place in a changing world.

Téllez-Valdés and Dávila-Aranda (2003) explored this issue for cacti, the dominant plant form in Mexico's Tehuacán-Cuicatlán Biosphere Reserve. From knowledge of the biophysical basis of current species distributions and assuming one of three future climate scenarios, they predicted future species distributions in relation to the location of the reserve. Table 14.3 shows how the potential ranges of species contracted or expanded in the various scenarios. Focusing on

**Table 14.3**

The core distributions (km<sup>2</sup>) of cacti in Mexico under current conditions and as predicted for three climate change scenarios. Species in the first category of cacti are currently completely restricted to the 10,000 km<sup>2</sup> Tehuacán-Cuicatlán Biosphere Reserve. Those in the second category have a current range more or less equally distributed inside and outside the reserve. The current ranges of species in the final category extend widely beyond the reserve boundaries.

SPECIES CATEGORY	CURRENT	+1.0°C –10% RAIN	+2.0°C –10% RAIN	+2.0°C –15% RAIN
<b>Restricted to the reserve</b>				
<i>Cephalocereus columna-trajani</i>	138	27	0	0
<i>Ferocactus flavovirens</i>	317	532	100	55
<i>Mammillaria huitzilopochtli</i>	68	21	0	0
<i>Mammillaria pectinifera</i>	5,130	1,124	486	69
<i>Pachycereus hollianus</i>	175	87	0	0
<i>Polaskia chende</i>	157	83	76	41
<i>Polaskia chichipe</i>	387	106	10	0
<b>Intermediate distribution</b>				
<i>Coryphantha pycnantha</i>	1,367	2,881	1,088	807
<i>Echinocactus platyacanthus f. grandis</i>	1,285	1,046	230	1,148
<i>Ferocactus haematacanthus</i>	340	1,979	1,220	170
<i>Pachycereus weberi</i>	2,709	3,492	1,468	1,012
<b>Widespread distribution</b>				
<i>Coryphantha pallida</i>	10,237	5,887	3,459	2,920
<i>Ferocactus recurvus</i>	3,220	3,638	1,651	151
<i>Mammillaria dioxanthocentron</i>	9,934	7,126	5,177	3,162
<i>Mammillaria polyedra</i>	10,118	5,512	3,473	2,611
<i>Mammillaria sphacelata</i>	3,956	5,440	2,803	2,580
<i>Neobuxbaumia macrocephala</i>	2,846	4,943	3,378	1,964
<i>Neobuxbaumia tetetzo</i>	2,964	1,357	519	395
<i>Pachycereus chrysacanthus</i>	1,395	1,929	872	382
<i>Pachycereus fulviceps</i>	3,306	5,405	2,818	1,071



the most extreme scenario (an average temperature increase of 2.0°C and a 15% reduction in rainfall), it is evident that more than half of the species that are currently restricted to the reserve are predicted to go extinct. A second category of cacti, whose current ranges are almost equally within and outside the reserve, are expected to contract their ranges, but in such a way that their distributions become almost completely confined to the reserve. A final category, whose current distributions are much more widespread, also suffer range contractions but in future they are still expected to be distributed within and outside the reserve. In the case of these cacti, then, the location of the reserve seems to cater adequately for potential range changes. But how many other nature reserves may turn out to be in the wrong place?

## 14.5 Finale

This final chapter has brought together a diversity of environmental problems (overexploitation, habitat disruption, introduced species, global climate change), which themselves require us to understand population, community and ecosystem dynamics. We have seen that the dynamics of endangered species are governed by a high level of uncertainty; despite this, our knowledge is sometimes sufficient to safeguard biodiversity.

Nevertheless, there is no room for complacency. We have insufficient knowledge and, just as important, insufficient financial resources to protect everything everywhere. In desperate times, painful decisions have to be made about priorities. Thus, wounded soldiers arriving at field hospitals in the First World War were subjected to a *triage* evaluation: priority 1, those who were likely to survive but only with rapid intervention; priority 2, those who were likely to survive without rapid intervention; priority 3, those who were likely to die with or without intervention. Conservation managers are often faced with the same kind of choices and need to demonstrate some courage in giving up on hopeless cases, and prioritizing those species and habitats where something can be done.

The spectrum of opinions on conservation is complete. It ranges from the environmental terrorist, who is prepared to destroy property and put human life at risk for what is seen as unacceptable exploitation of animals, to the other extreme of the exploitative terrorist, who is prepared to destroy a rare habitat just as it is about to achieve protected status. There are zealots on both sides of the spectrum too. On the one hand, there are the industrialists, fishers, farmers and foresters who accept none of the conservationist case and are not prepared to look objectively at the scientific evidence, while, on the other, are the environmental zealots – preservationists who seem unwilling to accept any exploitation of the natural world, some even pronouncing that fishing or hunting or logging are intrinsically wrong. The middle ground is occupied by both exploiters and conservationists whose basic philosophy holds that natural resources can be used, but this should be in a sustainable and balanced manner. A thorough understanding of the principles and applications of ecological science should enable all to pay healthy regard to the scientific aspects of what, in its broader context, is very much an ethical, economic and sociopolitical problem. The task for the next generation of ecologists is to bring their understanding to bear in this challenging environment.

the 'triage' approach to setting priorities

the challenge – taking a balanced view





## Summary

# SUMMARY

### The scale of the problem

Conservation is the science concerned with increasing the probability that the Earth's species and communities (or, more generally, its biodiversity) will persist into the future. Biodiversity is, at its most basic, the number of species present, but it can also be viewed at smaller scales (e.g. genetic variation within populations) and larger scales (e.g. the variety of community types present in a region). About 1.8 million species have so far been named, but the real number is probably between 3 and 30 million. The current observed rate of extinction may be as much as 100–1000 times the background rate indicated by the fossil record.

### Endangered species and rarity

A species may be rare in the sense that its geographic and/or habitat ranges are small or in the sense that local populations, even where they do occur, are small. Many species are naturally rare but just by virtue of their rarity species are not necessarily at risk of extinction. However, other things being equal, it will be easier to make a rare species extinct. Some species are born rare, others have rarity thrust upon them as a result of the actions of humans.

### Threats to biodiversity

The principal causes of decline are overexploitation, habitat degradation and the introduction of exotic species. Overexploitation occurs when people harvest a population (for food or trophies) at a rate that is unsustainable. Humans adversely affect habitat in three ways – a proportion of available habitat may simply be destroyed, or it may be degraded by pollution, or it may be disturbed by human activities to the detriment of some of its occupants. Human-caused introductions of exotic species, which may occur accidentally or intentionally, have sometimes been responsible for dramatic changes to native species and natural communities.

### Genetic problems

Rare alleles of a gene may confer no immediate advantage but could turn out to be well suited to changed environmental conditions in the future – small populations that have lost rare alleles through genetic drift have less potential to adapt. A more immediate potential problem is inbreeding depression – when populations are small there is a tendency for individuals breeding with one another to be related, and this may lead to reductions in fertility, survivorship, growth rates and resistance to disease.

### The extinction vortex

A given population may have been reduced to a very small size by one or more of the processes described above, and this may have led to an increased frequency of matings among relatives and the expression of deleterious recessive alleles in offspring, leading to reduced survivorship and fecundity and causing the population to become smaller still – the so-called extinction vortex.

### Conservation in practice

Much of conservation biology is a crisis discipline concerned with small populations in immediate danger of extinction. A high level of uncertainty governs the dynamics of small populations, whereas large populations can be described as being governed by 'the law of averages'. Three kinds of uncertainty or variation can be identified that are of particular importance to the fate of small populations: demographic uncertainty, environmental uncertainty and spatial uncertainty. Moreover, loss of habitat frequently results not only in a reduction in the absolute size of a population but also the division of the original population into a number of fragments.

### Predicting minimum viable population size

Population viability analysis, a simulation modeling tool, can be used to estimate the minimum population

size of a particular species that should ensure its persistence with an acceptable probability (e.g. greater than 90%) for a reasonable period (e.g. 100 years). Armed with such information, managers can work out the best approach to guard against extinction (supplementary feeding, predator control, one or more reserves of appropriate size, etc.)

### Selecting protected areas

Given limited funds to purchase protected areas, it is important to devise priorities so that they can be evaluated systematically and chosen with care. We know that the biotas of different locations vary in species richness, the extent to which the biota is unique and the extent to which the biota is endangered; one or more of these criteria could be used to prioritize potential areas for protection. The principles of island biogeography theory provide some clues about the most appropriate shape and disposition of protected areas. The selection of a network of reserves to optimize

the protection of biodiversity can be performed on the basis of 'complementarity' (selecting at each step the site that is most complementary to those already selected in terms of the biodiversity it contains) or 'irreplaceability' (defined in terms of the likelihood of an area being required to achieve specified conservation targets).

### Global climate change and conservation

Predicted changes to patterns of temperature and rainfall around the world have important implications for conservation biology. Changes to environmental conditions will affect the size and location of habitable areas of species, whether or not they are currently at risk of extinction. Moreover, nature reserves may turn out to be in the wrong places. Models of global climate change can be used by ecologists to safeguard species and communities when planning for the conservation of individual species or designing reserve networks.

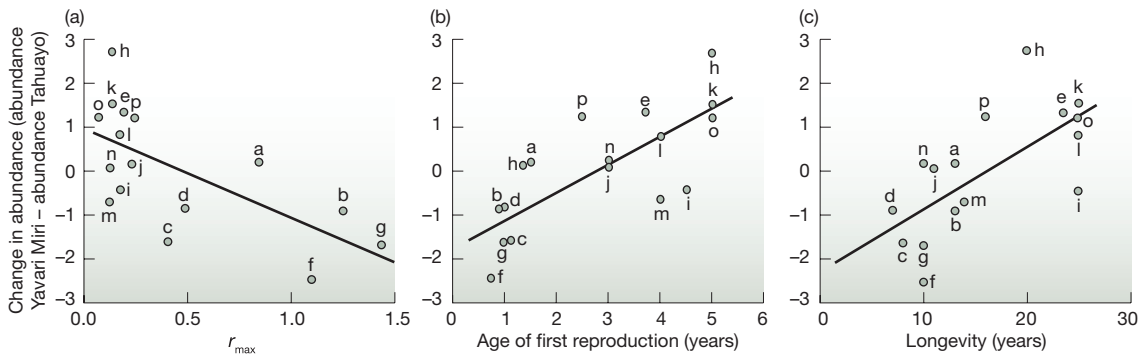
## Review questions

### REVIEW QUESTIONS

Asterisks indicate challenge questions

- 1\* Of the estimated 3–30 million species on Earth, only about 1.8 million have so far been named. How important is it for the conservation of biodiversity that we can name the species involved?
- 2 Species may be 'rare' on three counts: what are these? From your own experience, provide examples of three 'rare' species and explain the nature of their rarity.
- 3\* Researchers collected data on the relative abundance of 16 Peruvian mammal species

in forest areas that contrasted in whether they were subject to light or heavy hunting by local people. As an index of vulnerability to hunting they used the reduction in relative abundance in the heavily versus lightly hunted areas. This was plotted against intrinsic rate of population increase ( $r_{\max}$ ), age of first reproduction and longevity (Figure 14.15). Provide explanations for the relationships shown in the figure. Would you expect the variables  $r_{\max}$ , age of first reproduction and longevity to be intercorrelated? If so, how? Many species of large animals have gone extinct in the last 50,000 years. What light do the results of



**Figure 14.15**

Relationships between (a)  $r_{max}$ , (b) age of first reproduction, and (c) longevity and the vulnerability of mammals to population declines measured as the change in abundance between lightly and heavily hunted areas of forest. The mammals are represented by the following letters: a, white-lipped peccary; b, collared peccary; c, red brocket deer; d, gray brocket deer; e, lowland tapir; f, black agouti; g, green acouchy; h, woolly monkey; i, howler monkey; j, red wakari monkey; k, brown capuchin; l, white-fronted capuchin; m, monk saki monkey; n, titi monkey; o, spider monkey; p, squirrel monkey.

AFTER BODMER ET AL., 1997

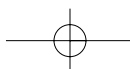
this study shed on the possible role of overexploitation by humans in historical extinctions? On the basis of these results, what advice would you give wildlife managers about conserving mammals in Peruvian forests?

- 4 Are there any circumstances where the intentional introduction of an exotic species can be considered a good thing because it enhances biodiversity?
- 5 Unpredictable temporal variability is a feature of most ecosystems. How can conservation biologists allow for such uncertainty when they devise species management plans?
- 6 Explain, with examples, how the loss or introduction of a single species can have conservation consequences throughout a whole ecological community.
- 7 In desperate times, painful decisions have to be made about priorities. Discuss the 'triage' approach to conservation assessment. List some highly endangered species of which you are aware and propose priorities for conservation action. Are any so hopeless that they should be allowed to go extinct?
- 8 Discuss the value of zoos and botanical gardens in nature conservation.
- 9 Discuss the advantages and limitations of using population viability analysis tools to devise species management plans.
- 10\* The famous ecologist of the early 20th century, A.G. Tansley, when asked what he meant by nature conservation, said it was maintaining the world in the state he knew as a child. From your perspective, as we enter the new millennium, how would you define the aims of conservation biology?



# References

- Abramsky, Z. & Rosenzweig, M.L. (1983) Tilman's predicted productivity–diversity relationship shown by desert rodents. *Nature*, 309, 150–151.
- Agrawal, A.A. (1998) Induced responses to herbivory and increased plant performance. *Science*, 279, 1201–1202.
- Akçakaya, H.R. (1992) Population viability analysis and risk assessment. In: *Proceedings of Wildlife 2001: Populations* (D.R. McCullough, ed.), pp. 148–157. Elsevier, Amsterdam.
- Al-Hiyaly, S.A., McNeilly, T. & Bradshaw, A.D. (1988) The effects of zinc contamination from electricity pylons – evolution in a replicated situation. *New Phytologist*, 110, 571–580.
- Allan, J.D. & Flecker, A.S. (1993) Biodiversity conservation in running waters. *Bioscience*, 43, 32–43.
- Alliende, M.C. & Harper, J.L. (1989) Demographic studies of a dioecious tree. I. Colonization, sex and age-structure of a population of *Salix cinerea*. *Journal of Ecology*, 77, 1029–1047.
- Anderson, R.M. (1982) Epidemiology. In: *Modern Parasitology* (F.E.G. Cox, ed.), pp. 205–251. Blackwell Scientific Publications, Oxford.
- Anderson, R.M. & May, R.M. (1991) *Infectious Diseases of Humans: Dynamics and Control*. Oxford University Press, Oxford.
- Andrewartha, H.G. (1961) *Introduction to the Study of Animal Populations*. Methuen, London.
- Angel, M.V. (1994) Spatial distribution of marine organisms: patterns and processes. In: *Large Scale Ecology and Conservation Biology* (P.J. Edwards, R.M. May & N.R. Webb, eds), pp. 59–109. Blackwell Science, Oxford.
- Arheimer, B. & Wittgren, H.B. (2002) Modelling nitrogen retention in potential wetlands at the catchment scale. *Ecological Engineering*, 19, 63–80.
- Aston, J.L. & Bradshaw, A.D. (1966) Evolution in closely adjacent plant populations. II. *Agrostis stolonifera* in maritime habitats. *Heredity*, 21, 649–664.
- Atkinson, D., Ciotti, B.J. & Montagnes, D.J.S. (2003) Protists decrease in size linearly with temperature: *ca.* 2.5%°C<sup>-1</sup>. *Proceedings of the Royal Society of London, Series B*, 270, 2605–2611.
- Audesirk, T. & Audesirk, G. (1996) *Biology: Life on Earth*. Prentice Hall, Upper Saddle River, NJ.
- Ayre, D.J. (1985) Localized adaptation of clones of the sea anemone *Actinia tenebrosa*. *Evolution*, 39, 1250–1260.
- Ayre, D.J. (1995) Localized adaptation of sea anemone clones: evidence from transplantation over two spatial scales. *Journal of Animal Ecology*, 64, 186–196.
- Bach, C.E. (1994) Effects of herbivory and genotype on growth and survivorship of sand-dune willow (*Salix cordata*). *Ecological Entomology*, 19, 303–309.
- Baker, A.J.M. (2002) The use of tolerant plants and hyperaccumulators. In: *The Restoration and Management of Derelict Land: Modern Approaches* (M.H. Wong & A.D. Bradshaw, eds), pp. 138–148. World Scientific Publishing, Singapore.
- Balmford, A. & Bond, W. (2005) Trends in the state of nature and their implications for human well-being. *Ecology Letters*, 8, 1218–1234.
- Balmford, A., Bruner, A., Cooper, P. et al. (2002) Economic reasons for conserving wild nature. *Science*, 297, 950–953.
- Barrios, L. & Rodriguez, A. (2004) Behavioural and environmental correlates of soaring-bird mortality at on-shore wind turbines. *Journal of Applied Ecology*, 41, 72–81.
- Bayliss, P. (1987) Kangaroo dynamics. In: *Kangaroos, their Ecology and Management in the Sheep Rangelands of Australia* (G. Caughley, N. Shepherd & J. Short, eds), pp. 119–134. Cambridge University Press, Cambridge.
- Bazzaz, F.A. (1979) The physiological ecology of plant succession. *Annual Review of Ecology and Systematics*, 10, 351–371.
- Bazzaz, F.A. (1996) *Plants in Changing Environments*. Cambridge University Press, Cambridge.
- Bazzaz, F.A., Miao, S.L. & Wayne, P.M. (1993) CO<sub>2</sub>-induced growth enhancements of co-occurring tree species decline at different rates. *Oecologia*, 96, 478–482.
- Bazzaz, F.A. & Williams, W.E. (1991) Atmospheric CO<sub>2</sub> concentrations within a mixed forest: implications for seedling growth. *Ecology*, 72, 12–16.
- Beaumont, L.J. & Hughes, L. (2002) Potential changes in the distributions of latitudinally restricted Australian butterfly species in response to climate change. *Global Change Biology*, 8, 954–971.
- Becker, P. (1992) Colonization of islands by carnivorous and herbivorous Heteroptera and Coleoptera: effects of island area, plant species richness, and 'extinction' rates. *Journal of Biogeography*, 19, 163–171.
- Begon, M., Sait, S.M. & Thompson, D.J. (1995) Persistence of a predator–prey system: refuges and generation cycles? *Proceedings of the Royal Society of London, Series B*, 260, 131–137.
- Begon, M., Townsend, C.R. & Harper, J.L. (2006) *Ecology: from Individuals to Ecosystems*, 4th edn. Blackwell Publishing, Oxford.
- Belt, T. (1874) *The Naturalist in Nicaragua*. J.M. Dent, London.





Berger, J. (1990) Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. *Conservation Biology*, 4, 91–98.

Berner, E.K. & Berner, R.A. (1987) *The Global Water Cycle: Geochemistry and Environment*. Prentice Hall, Englewood Cliffs, NJ.

Berven, K.A. (1995) Population regulation in the wood frog, *Rana sylvatica*, from three diverse geographic localities. *Australian Journal of Ecology*, 20, 385–392.

Blaustein, A.R., Wake, D.B. & Sousa, W.P. (1994) Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conservation Biology*, 8, 60–71.

Bobko, S.J. & Berkeley, S.A. (2004) Maturity, ovarian cycle, fecundity, and age-specific parturition of black rockfish (*Sebastes melanops*). *Fisheries Bulletin*, 102, 418–429.

Bodmer, R.E., Eisenberg, J.F. & Redford, K.H. (1997) Hunting and the likelihood of extinction of Amazonian mammals. *Conservation Biology*, 11, 460–466.

Bonnet, X., Lourdais, O., Shine, R. & Naulleau, G. (2002) Reproduction in a typical capital breeder: costs, currencies and complications in the aspic viper. *Ecology*, 83, 2124–2135.

Bonsall, M.B., French, D.R. & Hassell, M.P. (2002) Metapopulation structure affects persistence of predator–prey interactions. *Journal of Animal Ecology*, 71, 1075–1084.

Borga, K., Gabrielsen, G.W. & Skaare, J.U. (2001) Biomagnification of organochlorines along a Barents Sea food chain. *Environmental Pollution*, 113, 187–198.

Bouzille, J.B., Bonis, A., Clement, B. & Godeau, M. (1997) Growth patterns of *Juncus gerardi* clonal populations in a coastal habitat. *Plant Ecology*, 132, 39–48.

Bowles, K.C., Apte, S.C., Maher, W.A., Kawei, M. & Smith, R. (2001) Bioaccumulation and biomagnification of mercury in Lake Murray, Papua New Guinea. *Canadian Journal of Fisheries and Aquatic Science*, 58, 888–897.

Bradshaw, A.D. (2002) Introduction – an ecological perspective. In: *The Restoration and Management of Derelict Land: Modern Approaches* (M.H. Wong & A.D. Bradshaw, eds), pp. 1–6. World Scientific Publishing, Singapore.

Breznak, J.A. (1975) Symbiotic relationships between termites and their intestinal biota. In: *Symbiosis* (D.H. Jennings & D.L. Lee, eds), pp. 559–580. Symposium 29, Society for Experimental Biology. Cambridge University Press, Cambridge.

Briand, F. (1983) Environmental control of food web structure. *Ecology*, 64, 253–263.

Brook, B.W., O’Grady, J.J., Chapman, A.P., Burgman, M.A., Akçakaya, H.R. & Frankham, R. (2000) Predictive accuracy of population viability analysis in conservation biology. *Nature*, 404, 385–387.

Brookes, M. (1998) The species enigma. *New Scientist*, June 13, 1998.

Brown, J.H. & Davidson, D.W. (1977) Competition between seed-eating rodents and ants in desert ecosystems. *Science*, 196, 880–882.

Brown, V.K. & Southwood, T.R.E. (1983) Trophic diversity, niche breadth, and generation times of exopterygote insects in a secondary succession. *Oecologia*, 56, 220–225.

Brunet, A.K. & Medellín, R.A. (2001) The species–area relationship in bat assemblages of tropical caves. *Journal of Mammalogy*, 82, 1114–1122.

Brylinski, M. & Mann, K.H. (1973) An analysis of factors governing productivity in lakes and reservoirs. *Limnology and Oceanography*, 18, 1–14.

Buckling, A. & Rainey, P.B. (2002) Antagonistic coevolution between a bacterium and a bacteriophage. *Proceedings of the Royal Society of London, Series B*, 269, 931–936.

Bullock, J.M., Moy, I.L., Pywell, R.F., Coulson, S.J., Nolan, A.M. & Caswell, H. (2002) Plant dispersal and colonization processes at local and landscape scales. In: *Dispersal Ecology* (J.M. Bullock, R.E. Kenward & R.S. Hails, eds), pp. 279–302. Blackwell Publishing, Oxford.

Burdon, J.J. (1987) *Diseases and Plant Population Biology*. Cambridge University Press, Cambridge.

Burdon-Sanderson, J.S. (1893) *Inaugural address*. *Nature*, 48, 464–472.

Burg, T.M. & Croxall, J.P. (2001) Global relationships amongst black-browed and grey-headed albatrosses: analysis of population structure using mitochondrial DNA and microsatellites. *Molecular Ecology*, 10, 2647–2660.

Burgman, M.A., Ferson, S. & Akçakaya, H.R. (1993) *Risk Assessment in Conservation Biology*. Chapman & Hall, London.

Buscot, F., Munch, J.C., Charcosset, J.Y., Gardes, M., Nehls, U. & Hampp, R. (2000) Recent advances in exploring physiology and biodiversity of ectomycorrhizas highlight the functioning of these symbioses in ecosystems. *FEMS Microbiology Reviews*, 24, 601–614.

Cain, M.L., Pacala, S.W., Silander, J.A. & Fortin, M.-J. (1995) Neighbourhood models of clonal growth in the white clover *Trifolium repens*. *American Naturalist*, 145, 888–917.

Carignan, R., Planas, D. & Vis, C. (2000) Planktonic production and respiration in oligotrophic shield lakes. *Limnology and Oceanography*, 45, 189–199.

Carruthers, R.I., Larkin, T.S., Firstencel, H. & Feng, Z. (1992) Influence of thermal ecology on the mycosis of a rangeland grasshopper. *Ecology*, 73, 190–204.

Caughley, G. (1994) Directions in conservation biology. *Journal of Animal Ecology*, 63, 215–244.

Cebrian, J. (1999) Patterns in the fate of production in plant communities. *American Naturalist*, 154, 449–468.

Charnov, E.L. (1976) Optimal foraging: attack strategy of a mantid. *American Naturalist*, 110, 141–151.

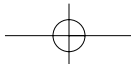
Chase, J.M. (2003) Experimental evidence for alternative stable equilibria in a benthic pond food web. *Ecology Letters*, 6, 733–741.

Choquenot, D. (1998) Testing the relative influence of intrinsic and extrinsic variation in food availability on feral pig populations in Australia’s rangelands. *Journal of Animal Ecology*, 67, 887–907.

Clements, F.L. (1905) *Research Methods in Ecology*. University of Nevada Press, Lincoln, NV.

Cohen, J.E. (1995) *How Many People Can the Earth Support?* W.W. Norton & Co., New York.

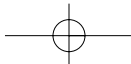
Cohen, J.E. (2001) World population in 2050: assessing the projections. In: *Seismic Shifts: the Economic Impact of Demographic Change* (J.S. Little & R.K. Triest, eds), pp. 83–113.







- Conference Series No. 48. Federal Reserve Bank of Boston, Boston.
- Cohen, J.E. (2003) Human population: the next half century. *Science*, 302, 1172–1175.
- Cohen, J.E. (2005) Human population grows up. *Scientific American*, 293(3), 48–55.
- Cole, J.J., Findlay, S. & Pace, M.L. (1988) Bacterial production in fresh and salt water ecosystems: a cross-system overview. *Marine Ecology Progress Series*, 4, 1–10.
- Connell, J.H. (1978) Diversity in tropical rainforests and coral reefs. *Science*, 199, 1302–1310.
- Connell, J.H. (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist*, 122, 661–696.
- Cook, L.M., Dennis, R.L.H. & Mani, G.S. (1999) Melanic morph frequency in the peppered moth in the Manchester area. *Proceedings of the Royal Society of London, Series B*, 266, 293–297.
- Coomes, D.A., Rees, M., Turnbull, L. & Ratcliffe, S. (2002) On the mechanisms of coexistence among annual-plant species, using neighbourhood techniques and simulation models. *Plant Ecology*, 163, 23–38.
- Cornell, H.V. & Hawkins, B.A. (2003) Herbivore responses to plant secondary compounds: a test of phytochemical coevolution theory. *American Naturalist*, 161, 507–522.
- Cortes, E. (2002) Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. *Conservation Biology*, 16, 1048–1062.
- Cory, J.S. & Myers, J.H. (2000) Direct and indirect ecological effects of biological control. *Trends in Ecology and Evolution*, 15, 137–139.
- Costanza, R., D’Arge, R., de Groot, R. et al. (1997) The value of the world’s ecosystem services and natural capital. *Nature*, 387, 253–260.
- Cotrufo, M.F., Ineson, P., Scott, A. et al. (1998) Elevated CO<sub>2</sub> reduces the nitrogen concentration of plant tissues. *Global Change Biology*, 4, 43–54.
- Cottingham, K.L., Brown, B.L. & Lennon, J.T. (2001) Biodiversity may regulate the temporal variability of ecological systems. *Ecology Letters*, 4, 72–85.
- Courchamp, F., Clutton-Brock, T. & Grenfell, B. (1999) Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution*, 14, 405–410.
- Cowling, R.M., Pressey, R.L., Rouget, M. & Lombard, A.T. (2003) A conservation plan for a global biodiversity hotspot – the Cape Floristic Region, South Africa. *Biological Conservation*, 112, 191–216.
- Cox, P.A., Elmquist, T., Pierson, E.D. & Rainey, W.E. (1991) Flying foxes as strong interactors in South Pacific island ecosystems: a conservation hypothesis. *Conservation Biology*, 5, 448–454.
- Crisp, M.D. & Lange, R.T. (1976) Age structure distribution and survival under grazing of the arid zone shrub *Acacia burkitii*. *Oikos*, 27, 86–92.
- Currie, D.J. (1991) Energy and large-scale patterns of animal and plant species richness. *American Naturalist*, 137, 27–49.
- Currie, D.J. & Paquin, V. (1987) Large-scale biogeographical patterns of species richness in trees. *Nature*, 39, 326–327.
- Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection*, 1st edn. John Murray, London.
- Davidson, D.W. (1977) Species diversity and community organization in desert seed-eating ants. *Ecology*, 58, 711–724.
- Davidson, J. & Andrewartha, H.G. (1948) The influence of rainfall, evaporation and atmospheric temperature on fluctuations in the size of a natural population of *Thrips imaginis* (Thysanoptera). *Journal of Animal Ecology*, 17, 200–222.
- Davies, S.J., Palmiotto, P.A., Ashton, P.S., Lee, H.S. & Lafrankie, J.V. (1998) Comparative ecology of 11 sympatric species of *Macaranga* in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. *Journal of Ecology*, 86, 662–673.
- Davis, M.B. (1976) Pleistocene biogeography of temperate deciduous forest. *Geoscience and Management*, 13, 13–26.
- Davis, M.B. & Shaw, R.G. (2001) Range shifts and adaptive responses to quaternary climate change. *Science*, 292, 673–679.
- de Wit, C.T. (1965) Photosynthesis of leaf canopies. *Verslagen van Landbouwkundige Onderzoekingen*, 663, 1–57.
- de Wit, C.T., Tow, P.G. & Ennik, G.C. (1966) Competition between legumes and grasses. *Verslagen van Landbouwkundige Onderzoekingen*, 112, 1017–1045.
- Deevey, E.S. (1947) Life tables for natural populations of animals. *Quarterly Review of Biology*, 22, 283–314.
- Denno, R.F., McClure, M.S. & Ott, J.R. (1995) Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annual Review of Entomology*, 40, 297–331.
- Detwiler, R.P. & Hall, C.A.S. (1988) Tropical forests and the global carbon cycle. *Science*, 239, 42–47.
- Diamond, J.M. (1972) Biogeographic kinetics: estimation of relaxation times for avifaunas of south-west Pacific islands. *Proceedings of the National Academy of Science of the USA*, 69, 3199–3203.
- Dickie, I.A., Xu, B. & Koide, R.T. (2002) Vertical niche differentiation of ectomycorrhizal hyphae in soil as shown by T-RFLP analysis. *New Phytologist*, 156, 527–535.
- Dobson, A.P. & Carper, E.R. (1996) Infectious diseases and human population history. *Bioscience*, 46, 115–126.
- Dodson, S.I., Arnott, S.E. & Cottingham, K.L. (2000) The relationship in lake communities between primary productivity and species richness. *Ecology*, 81, 2662–2679.
- Doube, B.M., Macqueen, A., Ridsdill-Smith, T.J. & Weir, T.A. (1991) Native and introduced dung beetles in Australia. In: *Dung Beetle Ecology* (I. Hanski & Y. Cambefort, eds), pp. 255–278. Princeton University Press, Princeton, NJ.
- Drès, M. & Mallet, J. (2001) Host races in plant-feeding insects and their importance in sympatric speciation. *Philosophical Transactions of the Royal Society of London, Series B*, 357, 471–492.
- Dunne, J.A., Williams, R.J. & Martinez, N.J. (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, 5, 558–567.
- Eamus, D. (1999) Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. *Trends in Ecology and Evolution*, 14, 11–16.
- Ebert, D., Zschokke-Rohringer, C.D. & Carius, H.J. (2000) Dose effects and density-dependent regulation in two micro-parasites of *Daphnia magna*. *Oecologia*, 122, 200–209.





Ehrlich, P. & Raven, P.H. (1964) Butterflies and plants: a study in coevolution. *Evolution*, 18, 586–608.

Eis, S., Garman, E.H. & Ebel, L.F. (1965) Relation between cone production and diameter increment of douglas fir (*Pseudotsuga menziesii* (Mirb). Franco), grand fir (*Abies grandis* Dougl.) and western white pine (*Pinus monticola* Dougl.). *Canadian Journal of Botany*, 43, 1553–1559.

Elliott, J.K. & Mariscal, R.N. (2001) Coexistence of nine anemonefish species: differential host and habitat utilization, size and recruitment. *Marine Biology*, 138, 23–36.

Elliott, J.M. (1994) *Quantitative Ecology and the Brown Trout*. Oxford University Press, Oxford.

Elton, C. (1927) *Animal Ecology*. Sidgwick & Jackson, London.

Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*. Methuen, London.

Endler, J.A. (1980) Natural selection on color patterns in *Poecilia reticulata*. *Evolution*, 34, 76–91.

Erwin, T.L. (1982) Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopterists Bulletin*, 36, 74–75.

Falge, E., Baldocchi, D., Tenhunen, J. et al. (2002) Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agricultural and Forest Meteorology*, 113, 53–74.

Fasham, M.J.R., Balino, B.M. & Bowles, M.C. (2001) A new vision of ocean biogeochemistry after a decade of the Joint Global Ocean Flux Study (JGOFS). *Ambio Special Report*, 10, 4–31.

Fenner, F. (1983) Biological control, as exemplified by smallpox eradication and myxomatosis. *Proceedings of the Royal Society, Series B*, 218, 259–285.

Ferguson, R.G. (1933) The Indian tuberculosis problem and some preventative measures. *National Tuberculosis Association Transactions*, 29, 93–106.

Fischer, M. & Matthies, D. (1998) Effects of population size on performance in the rare plant *Gentianella germanica*. *Journal of Ecology*, 86, 195–204.

FitzGibbon, C.D. (1990) Anti-predator strategies of immature Thomson's gazelles: hiding and the prone response. *Animal Behaviour*, 40, 846–855.

FitzGibbon, C.D. & Fanshawe, J. (1989) The condition and age of Thomson's gazelles killed by cheetahs and wild dogs. *Journal of Zoology*, 218, 99–107.

Flecker, A.S. & Townsend, C.R. (1994) Community-wide consequences of trout introduction in New Zealand streams. *Ecological Applications*, 4, 798–807.

Fleischer, R.C., Perry, E.A., Muralidharan, K., Stevens, E.E. & Wemmer, C.M. (2001) Phylogeography of the Asian elephant (*Elephas maximus*) based on mitochondrial DNA. *Evolution*, 55, 1882–1892.

Flessa, K.W. & Jablonski, D. (1995) Biogeography of recent marine bivalve mollusks and its implications of paleobiogeography and the geography of extinction: a progress report. *Historical Biology*, 10, 25–47.

Flint, M.L. & van den Bosch, R. (1981) *Introduction to Integrated Pest Management*. Plenum Press, New York.

Flower, R.J., Rippey, B., Rose, N.L., Appleby, P.G. & Battarbee, R.W. (1994) Palaeolimnological evidence for the acidification and contamination of lakes by atmospheric pollution in western Ireland. *Journal of Ecology*, 82, 581–596.

Fonseca, C.R. (1994) Herbivory and the long-lived leaves of an Amazonian ant-tree. *Journal of Ecology*, 82, 833–842.

Fonseca, D.M. & Hart, D.D. (1996) Density-dependent dispersal of black fly neonates is mediated by flow. *Oikos*, 75, 49–58.

Ford, E.B. (1975) *Ecological Genetics*, 4th edn. Chapman & Hall, London.

Ford, M.J. (1982) *The Changing Climate: Responses of the Natural Fauna and Flora*. George Allen & Unwin, London.

Fowler, S.V. (2004) Biological control of an exotic scale, *Orthozia insignis* Browne (Homoptera: Orthoxiidae), saves the endemic gumwood tree, *Commidendrum robustum* (Roxb.) DC (Asteraceae) on the island of St Helena. *Biological Control*, 29, 367–374.

Fox, C.J. (2001) Recent trends in stock-recruitment of blackwater herring (*Clupea harengus* L.) in relation to larval production. *ICES Journal of Marine Science*, 58, 750–762.

Fox, N.J. & Beckley, L.E. (2005) Priority areas for conservation of Western Australian coastal fishes: a comparison of hotspot, biogeographical and complementarity approaches. *Biological Conservation*, 125, 399–410.

Franklin, I.R. & Frankham, R. (1998) How large must populations be to retain evolutionary potential? *Animal Conservation*, 1, 69–73.

Fredrickson, R.J. & Hedrick, P.W. (2006) Dynamics of hybridization and introgression in red wolves and coyotes. *Conservation Biology*, 20, 1272–1283.

Gadgil, M. (1971) Dispersal: population consequences and evolution. *Ecology*, 52, 253–261.

Galloway, L.F. & Fenster, C.B. (2000) Population differentiation in an annual legume: local adaptation. *Evolution*, 54, 1173–1181.

Garthe, S. & Huppopp, O. (2004) Scaling possible adverse effects of marine wind farms on seabirds: developing and applying a vulnerability index. *Journal of Applied Ecology*, 41, 724–734.

Gaston, K.J. (1998) *Biodiversity*. Blackwell Science, Oxford.

Geider, R.J., Delucia, E.H., Falkowski, P.G. et al. (2001) Primary productivity of planet earth: biological determinants and physical constraints in terrestrial and aquatic habitats. *Global Change Biology*, 7, 849–882.

Gende, S.M., Quinn, T.P. & Willson, M.F. (2001) Consumption choice by bears feeding on salmon. *Oecologia*, 127, 372–382.

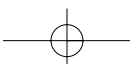
Gilman, M.P. & Crawley, M.J. (1990) The cost of sexual reproduction in ragwort (*Senecio jacobaea* L.). *Functional Ecology*, 4, 585–589.

Godfray, H.C.J. & Crawley, M.J. (1998) Introductions. In: *Conservation Science and Action* (W.J. Sutherland, ed.), pp. 39–65. Blackwell Science, Oxford.

Gotelli, N.J. & McCabe, D.J. (2002) Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules model. *Ecology*, 83, 2091–2096.

Gotthard, K., Nylin, S. & Wiklund, C. (1999) Seasonal plasticity in two satyrine butterflies: state-dependent decision making in relation to daylength. *Oikos*, 84, 453–462.

Gould, W.A. & Walker, M.D. (1997) Landscape-scale patterns in plant species richness along an arctic river. *Canadian Journal of Botany*, 75, 1748–1765.







References

Grant, P.R., Grant, B.R., Keller, L.F. & Petren, K. (2000) Effects of El Nino events on Darwin's finch productivity. *Ecology*, 81, 2442–2457.

Gray, S.M. & Robinson, B.W. (2001) Experimental evidence that competition between stickleback species favours adaptive character divergence. *Ecology Letters*, 5, 264–272.

Green, R.E. (1998) Long-term decline in the thickness of eggshells of thrushes, *Turdus* spp., in Britain. *Proceedings of the Royal Society of London, Series B*, 265, 679–684.

Green, R.E., Newton, I., Shultz, S., Cunningham, A.A., Gilbert, M., Pain, D.J. & Prakash, V. (2004) Diclofenac poisoning as a cause of vulture population declines across the Indian sub-continent. *Journal of Applied Ecology*, 41, 793–800.

Greenwood, P.J., Harvey, P.H. & Perrins, C.M. (1978) Inbreeding and dispersal in the great tit. *Nature*, 271, 52–54.

Gutter, A.S. (1999) Cleaner fish really do clean. *Nature*, 398, 672–673.

Grytnes, J.A. & Vetaas, O.R. (2002) Species richness and altitude: a comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *American Naturalist*, 159, 294–304.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960) Community structure, population control, and competition. *American Naturalist*, 44, 421–425.

Halaj, J., Ross, D.W. & Moldenke, A.R. (2000) Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. *Oikos*, 90, 139–152.

Hall, S.J. (1998) Closed areas for fisheries management – the case consolidates. *Trends in Ecology and Evolution*, 13, 297–298.

Hall, S.J. & Raffaelli, D.G. (1993) Food webs: theory and reality. *Advances in Ecological Research*, 24, 187–239.

Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, Oxford.

Hanski, I., Pakkala, T., Kuussaari, M. & Lei, G. (1995) Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos*, 72, 21–28.

Harcourt, D.G. (1971) Population dynamics of *Leptinotarsa decemlineata* (Say) in eastern Ontario. III. Major population processes. *Canadian Entomologist*, 103, 1049–1061.

Harper, J.L. (1977) *The Population Biology of Plants*. Academic Press, London.

Harper, J.L. & White, J. (1974) The demography of plants. *Annual Review of Ecology and Systematics*, 5, 419–463.

Hart, A.J., Bale, J.S., Tullett, A.G., Worland, M.R. & Walters, K.F.A. (2002) Effects of temperature on the establishment potential of the predatory mite *Amblyseius californicus* McGregor (Acari: Phytoseiidae) in the UK. *Journal of Insect Physiology*, 48, 593–599.

Hassell, M.P., Latto, J. & May, R.M. (1989) Seeing the wood for the trees: detecting density dependence from existing life-table studies. *Journal of Animal Ecology*, 58, 883–892.

Herman, T.J.B. (2000) Developing IPM for potato tuber moth. *Commercial Grower*, 55, 26–28.

Hermannsson, S. (2000) *Surtsey Research Report No. XI*. Museum of Natural History, Reykjavik, Iceland.

Hermoyian, C.S., Leighton, L.R. & Kaplan, P. (2002) Testing the role of competition in fossil communities using limiting similarity. *Geology*, 30, 15–18.

Herre, E.A. & West, S.A. (1997) Conflict of interest in a mutualism: documenting the elusive fig wasp–seed trade-off. *Proceedings of the Royal Society of London, Series B*, 264, 1501–1507.

Hilborn, R. & Walters, C.J. (1992) *Quantitative Fisheries Stock Assessment*. Chapman & Hall, New York.

Holloway, J.D. (1977) *The Lepidoptera of Norfolk Island, their Biogeography and Ecology*. Junk, The Hague.

Holloway, J.M., Dahlgren, R.A., Hansen, B. & Casey, W.H. (1998) Contribution of bedrock nitrogen to high nitrate concentrations in stream water. *Nature*, 395, 785–788.

Holyoak, M. & Lawler, S.P. (1996) Persistence of an extinction-prone predator–prey interaction through metapopulation dynamics. *Ecology*, 77, 1867–1879.

Hooper, D.U., Chapin, F.S., Ewel, J.J. et al. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, 75, 3–35.

Hoyer, M.V. & Canfield, D.E. (1994) Bird abundance and species richness on Florida lakes: influence of trophic status, lake morphology and aquatic macrophytes. *Hydrobiologia*, 297, 107–119.

Hudson, P.J., Dobson, A.P. & Newborn, D. (1992) Do parasites make prey vulnerable to predation? Red grouse and parasites. *Journal of Animal Ecology*, 61, 681–692.

Hudson, P.J., Dobson, A.P. & Newborn, D. (1998) Prevention of population cycles by parasite removal. *Science*, 282, 2256–2258.

Huffaker, C.B. (1958) Experimental studies on predation: dispersion factors and predator–prey oscillations. *Hilgardia*, 27, 343–383.

Hughes, L. (2000) Biological consequences of global warming: is the signal already apparent. *Trends in Ecology and Evolution*, 15, 56–61.

Hunter, M.L. & Yonzon, P. (1992) Altitudinal distributions of birds, mammals, people, forests, and parks in Nepal. *Conservation Biology*, 7, 420–423.

Hurd, L.E. & Eisenberg, R.M. (1990) Experimentally synchronized phenology and interspecific competition in mantids. *American Midland Naturalist*, 124, 390–394.

Hurn, A.D. (1998) Ecosystem-level evidence for top-down and bottom-up control of production in a grassland stream system. *Oecologia*, 115, 173–183.

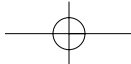
Husband, B.C. & Barrett, S.C.H. (1996) A metapopulation perspective in plant population biology. *Journal of Ecology*, 84, 461–469.

Hut, R.A., Barnes, B.M. & Daan, S. (2002) Body temperature patterns before, during and after semi-natural hibernation in the European ground squirrel. *Journal of Comparative Physiology B*, 172, 47–58.

Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbour Symposium on Quantitative Biology*, 22, 415–427.

Inouye, R.S., Huntly, N.J., Tilman, D., Tester, J.R., Stillwell, M. & Zinnel, K.C. (1987) Old-field succession on a Minnesota sand plain. *Ecology*, 68, 12–26.

Inouye, R.S. & Tilman, D. (1995) Convergence and divergence of old-field vegetation after 11 yr of nitrogen addition. *Ecology*, 76, 1872–1877.





Interlandi, S.J. & Kilham, S.S. (2001) Limiting resources and the regulation of diversity in phytoplankton communities. *Ecology*, 82, 1270–1282.

International Organisation for Biological Control (1989) *Current Status of Integrated Farming Systems Research in Western Europe* (P. Vereijken & D.J. Royle, eds). IOBC West Palaearctic Regional Service Bulletin No. 12(5). IOBC, Zurich.

IPCC (2001) *Third Assessment Report*. Working Group 1, Intergovernmental Panel on Climate Change. IPCC, Geneva.

Irvine, R.J., Stien, A., Dallas, J.F., Halvorsen, O., Langvatn, R. & Albon, S.D. (2001) Contrasting regulation of fecundity in two abomasal nematodes of Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Parasitology*, 122, 673–681.

IUCN/UNEP/WWF (1991) *Caring for the Earth. A Strategy for Sustainable Living*. World Conservation Union/United Nations Environmental Program/World Wide Fund, Gland, Switzerland.

Jackson, S.T. & Weng, C. (1999) Late quaternary extinction of a tree species in eastern North America. *Proceedings of the National Academy of Sciences of the USA*, 96, 13847–13852.

Jain, S.K. & Bradshaw, A.D. (1966) Evolutionary divergence among adjacent plant populations. I. The evidence and its theoretical analysis. *Heredity*, 21, 407–411.

Janis, C.M. (1993) Tertiary mammal evolution in the context of changing climates, vegetation and tectonic events. *Annual Review of Ecology and Systematics*, 24, 467–500.

Jennings, S., Kaiser, M.J. & Reynolds, J.D. (2001) *Marine Fisheries Ecology*. Blackwell Publishing, Oxford.

Jeppesen, E., Sondergaard, M., Jensen, J.P. et al. (2005) Lake responses to reduced nutrient loading – an analysis of contemporary long-term data from 35 case studies. *Freshwater Biology*, 50, 1747–1771.

Johannes, R.E. (1998) Government-supported village-based management of marine resources in Vanuatu. *Ocean Coastal Management*, 40, 165–186.

Johnson, C.G. (1967) International dispersal of insects and insect-borne viruses. *Netherlands Journal of Plant Pathology*, 73 (Suppl. 1), 21–43.

Johnson, J.A., Toepfer, J.E. & Dunn, P.O. (2003) Contrasting patterns of mitochondrial and microsatellite population structure in fragmented populations of greater prairie-chickens. *Molecular Ecology*, 12, 3335–3347.

Jones, M. & Harper, J.L. (1987) The influence of neighbours on the growth of trees. I. The demography of buds in *Betula pendula*. *Proceedings of the Royal Society of London, Series B*, 232, 1–18.

Jonsson, M. & Malmqvist, B. (2000) Ecosystem process rate increases with animal species richness: evidence from leaf-eating, aquatic insects. *Oikos*, 89, 519–523.

Jutila, H.M. (2003) Germination in Baltic coastal wetland meadows: similarities and differences between vegetation and seed bank. *Plant Ecology*, 166, 275–293.

Kaiser, J. (2000) Rift over biodiversity divides ecologists. *Science*, 89, 1282–1283.

Kamijo, T., Kitayama, K., Sugawara, A., Urushimichi, S. & Sasai, K. (2002) Primary succession of the warm-temperate broad-leaved forest on a volcanic island, Miyake-jima, Japan. *Folia Geobotanica*, 37, 71–91.

Karban, R., Agrawal, A.A., Thaler, J.S. & Adler, L.S. (1999) Induced plant responses and information content about risk of herbivory. *Trends in Ecology and Evolution*, 14, 443–447.

Karels, T.J. & Boonstra, R. (2000) Concurrent density dependence and independence in populations of arctic ground squirrels. *Nature*, 408, 460–463.

Karl, B.J. & Best, H.A. (1982) Feral cats on Stewart Island: their foods, and their effects on kakapo. *New Zealand Journal of Zoology*, 9, 287–294.

Karlsson, P.S. & Jacobson, A. (2001) Onset of reproduction in *Rhododendron lapponicum* shoots: the effect of shoot size, age, and nutrient status at two subarctic sites. *Oikos*, 94, 279–286.

Kerbes, R.H., Kotanen, P.M. & Jefferies, R.L. (1990) Destruction of wetland habitats by lesser snow geese: a keystone species on the west coast of Hudson Bay. *Journal of Applied Ecology*, 27, 242–258.

Kettlewell, H.B.D. (1955) Selection experiments on industrial melanism in the Lepidoptera. *Heredity*, 9, 323–342.

Khan, A.S., Sumaila, U.R., Watson, R., Munro, G. & Pauly, D. (2006) The nature and magnitude of global non-fuel fisheries subsidies. In: *Catching More Bait: a Bottom-up Re-estimation of Global Fisheries Subsidies* (U.R. Sumaila & D. Pauly, eds), pp. 5–37. Fisheries Centre Research Reports Vol. 14, No. 6. Fisheries Centre, University of British Columbia, Vancouver.

Kicklighter, D.W., Bruno, M., Donges, S. et al. (1999) A first-order analysis of the potential role of CO<sub>2</sub> fertilization to affect the global carbon budget: a comparison of four terrestrial biosphere models. *Tellus*, 51B, 343–366.

Kirk, J.T.O. (1994) *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge University Press, Cambridge, UK.

Kodric-Brown, A. & Brown, J.M. (1993) Highly structured fish communities in Australian desert springs. *Ecology*, 74, 1847–1855.

Krebs, C.J. (1972) *Ecology*. Harper & Row, New York.

Krebs, C.J., Boonstra, R., Boutin, S. & Sinclair, A.R.E. (2001) What drives the 10-year cycle of snowshoe hares? *Bioscience*, 51, 25–35.

Krebs, C.J., Sinclair, A.R.E., Boonstra, R., Boutin, S., Martin, K. & Smith, J.N.M. (1999) Community dynamics of vertebrate herbivores: how can we untangle the web? In: *Herbivores: between Plants and Predators* (H. Olff, V.K. Brown & R.H. Drent, eds), pp. 447–473. Blackwell Science, Oxford.

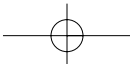
Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P. & Thorp, R.W. (2004) The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecology Letters*, 7, 1109–1119.

Kullberg, C. & Ekman, J. (2000) Does predation maintain tit community diversity? *Oikos*, 89, 41–45.

Lacy, R.C. (1993) VORTEX: a computer simulation for use in population viability analysis. *Wildlife Research*, 20, 45–65.

Lande, R. & Barrowclough, G.F. (1987) Effective population size, genetic variation, and their use in population management. In: *Viable Populations for Conservation* (M.E. Soulé, ed.), pp. 87–123. Cambridge University Press, Cambridge.

Larcher, W. (1980) *Physiological Plant Ecology*, 2nd edn. Springer-Verlag, Berlin.





References

Lathrop, R.C., Johnson, B.M., Johnson, T.B. et al. (2002) Stocking piscivores to improve fishing and water clarity: a synthesis of the Lake Mendota biomanipulation project. *Freshwater Biology*, 47, 2410–2424.

Laurance, W.F. (2001) Future shock: forecasting a grim fate for the Earth. *Trends in Ecology and Evolution*, 16, 531–533.

Law, B.E., Thornton, P.E., Irvine, J., Anthoni, P.M. & van Tuyl, S. (2001) Carbon storage and fluxes in ponderosa pine forests at different developmental stages. *Global Climate Change*, 7, 755–777.

Lawlor, L.R. (1980) Structure and stability in natural and randomly constructed competitive communities. *American Naturalist*, 116, 394–408.

Lawrence, W.H. & Rediske, J.H. (1962) Fate of sown douglas-fir seed. *Forest Science*, 8, 211–218.

Lawton, J.H. & May, R.M. (1984) The birds of Selborne. *Nature*, 306, 732–733.

Le Cren, E.D. (1973) Some examples of the mechanisms that control the population dynamics of salmonid fish. In: *The Mathematical Theory of the Dynamics of Biological Populations* (M.S. Bartlett & R.W. Hiorns, eds), pp. 125–135. Academic Press, London.

Lehmann, N., Eisenhawer, A., Hansen, K., Mech, L.D., Peterson, R.O., Gogan, P.J.P. & Wayne, R.K. (1991) Introgression of mitochondrial DNA into sympatric North American grey wolf population. *Evolution*, 45, 104–119.

Lennartsson, T., Nilsson, P. & Tuomi, J. (1998) Induction of overcompensation in the field gentian, *Gentiana campestris*. *Ecology*, 79, 1061–1072.

Leroy, F. & de Vuyst, L. (2001) Growth of the bacteriocin-producing *Lactobacillus sakei* strain CTC 494 in MRS broth is strongly reduced due to nutrient exhaustion: a nutrient depletion model for the growth of lactic acid bacteria. *Applied and Environmental Microbiology*, 67, 4407–4413.

Letourneau, D.K. & Dyer, L.A. (1998a) Density patterns of *Piper* ant-plants and associated arthropods: top-predator trophic cascades in a terrestrial system? *Biotropica*, 30, 162–169.

Letourneau, D.K. & Dyer, L.A. (1998b) Experimental test in a lowland tropical forest shows top-down effects through four trophic levels. *Ecology*, 79, 1678–1687.

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, 15, 237–240.

Lichter, J. (2000) Colonization constraints during primary succession on coastal Lake Michigan sand dunes. *Journal of Ecology*, 88, 825–839.

Likens, G.E. (1989) Some aspects of air pollutant effects on terrestrial ecosystems and prospects for the future. *Ambio*, 18, 172–178.

Likens, G.E. (1992) *The Ecosystem Approach: its Use and Abuse. Excellence in Ecology*, Book 3. Ecology Institute, Oldendorf-Luhe, Germany.

Likens, G.E. & Bormann, F.G. (1975) An experimental approach to New England landscapes. In: *Coupling of Land and Water Systems* (A.D. Hasler, ed.), pp. 7–30. Springer-Verlag, New York.

Likens, G.E. & Bormann, F.H. (1994) *Biogeochemistry of a Forested Ecosystem*, 2nd edn. Springer-Verlag, New York.

Likens, G.E., Bormann, F.H., Pierce, R.S. & Fisher, D.W. (1971) Nutrient–hydrologic cycle interaction in small forested watershed ecosystems. In: *Productivity of Forest Ecosystems* (P. Duvogneau, ed.), pp. 553–563. UNESCO, Paris.

Likens, G.E., Driscoll, C.T. & Buso, D.C. (1996) Long-term effects of acid rain: response and recovery of a forest ecosystem. *Science*, 272, 244–245.

Lindeman, R.L. (1942) The trophic–dynamic aspect of ecology. *Ecology*, 23, 399–418.

Lofgren, A. & Jerling, L. (2002) Species richness, extinction and immigration rates of vascular plants on islands in the Stockholm Archipelago, Sweden, during a century of ceasing management. *Folia Geobotanica*, 37, 297–308.

Lotka, A.J. (1932) The growth of mixed population: two species competing for a common food supply. *Journal of the Washington Academy of Sciences*, 22, 461–469.

Louda, S.M. (1982) Distributional ecology: variation in plant recruitment over a gradient in relation to insect seed predation. *Ecological Monographs*, 52, 25–41.

Louda, S.M. (1983) Seed predation and seedling mortality in the recruitment of a shrub, *Haplopappus venetus* (Asteraceae), along a climatic gradient. *Ecology*, 64, 511–521.

Louda, S.M., Kendall, D., Connor, J. & Simberloff, D. (1997) Ecological effects of an insect introduced for the biological control of weeds. *Science*, 277, 1088–1090.

Lövei, G.L. (1997) Global change through invasion. *Nature*, 388, 627–628.

Lubchenco, J. (1978) Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *American Naturalist*, 112, 23–39.

Lubchenco, J., Olson, A.M., Brubaker, L.B. et al. (1991) The sustainable biosphere initiative: an ecological research agenda. *Ecology*, 72, 371–412.

Luckman, W.H. & Decker, G.C. (1960) A 5-year report on observations in the Japanese beetle control area of Sheldon, Illinois. *Journal of Economic Entomology*, 53, 821–827.

Lussenhop, J. (1992) Mechanisms of microarthropod–microbial interactions in soil. *Advances in Ecological Research*, 23, 1–33.

MacArthur, J.W. (1975) Environmental fluctuations and species diversity. In: *Ecology and Evolution of Communities* (M.L. Cody & J.M. Diamond, eds), pp. 74–80. Belknap, Cambridge, MA.

MacArthur, R.H. (1955) Fluctuations of animal populations and a measure of community stability. *Ecology*, 36, 533–536.

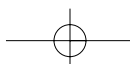
MacArthur, R.H. (1972) *Geographical Ecology*. Harper & Row, New York.

MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *American Naturalist*, 100, 603–609.

MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.

MacLulich, D.A. (1937) Fluctuations in numbers of the varying hare (*Lepus americanus*). *University of Toronto Studies, Biology Series*, 43, 1–136.

Malmqvist, B., Wotton, R.S. & Zhang, Y. (2001) Suspension feeders transform massive amounts of seston in large northern rivers. *Oikos*, 92, 35–43.





Malthus, T. (1798) *An Essay on the Principle of Population*. J. Johnson, London.

Martin, P.R. & Martin, T.E. (2001) Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. *Ecology*, 82, 189–206.

Martin, P.S. (1984) Prehistoric overkill: the global model. In: *Quaternary Extinctions: a Prehistoric Revolution* (P.S. Martin & R.G. Klein, eds), pp. 354–403. University of Arizona Press, Tuscon, AZ.

Marzusch, K. (1952) Untersuchungen über di Temperaturabhängigkeit von Lebensprozessen bei Insekten unter besonderer Berücksichtigung winter-schlantender Kartoffelkäfer. *Zeitschrift für vergleichende Physiologie*, 34, 75–92.

May, R.M. (1981) Patterns in multi-species communities. In: *Theoretical Ecology: Principles and Applications*, 2nd edn (R.M. May, ed.), pp. 197–227. Blackwell Scientific Publications, Oxford.

McGrady-Steed, J., Harris, P.M. & Morin, P.J. (1997) Biodiversity regulates ecosystem predictability. *Nature*, 390, 162–165.

McIntosh, A.R. & Townsend, C.R. (1994) Interpopulation variation in mayfly antipredator tactics: differential effects of contrasting predatory fish. *Ecology*, 75, 2078–2090.

McIntosh, A.R. & Townsend, C.R. (1996) Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behavior. *Oecologia*, 108, 174–181.

McKane, R.B., Johnson, L.C., Shaver, G.R. et al. (2002) Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*, 415, 68–71.

McKay, J.K., Bishop, J.G., Lin, J.-Z., Richards, J.H., Sala, A. & Mitchell-Olds, T. (2001) Local adaptation across a climatic gradient despite small effective population size in the rare sapphire rockcress. *Proceedings of the Royal Society of London, Series B*, 268, 1715–1721.

McKey, D. (1979) The distribution of secondary compounds within plants. In: *Herbivores: their Interaction with Secondary Plant Metabolites* (G.A. Rosenthal & D.H. Janzen, eds), pp. 56–134. Academic Press, New York.

Menges, E.S. (2000) Population viability analyses in plants: challenges and opportunities. *Trends in Ecology and Evolution*, 15, 51–56.

Menges, E.S. & Dolan, R.W. (1998) Demographic viability of populations of *Silene regia* in midwestern prairies: relationships with fire management, genetic variation, geographic location, population size and isolation. *Journal of Ecology*, 86, 63–78.

Merryweather, J.W. & Fitter, A.H. (1995) Phosphorus and carbon budgets: mycorrhizal contribution in *Hyacinthoides non-scripta* (L.) Chouard ex Rothm. under natural conditions. *New Phytologist*, 129, 619–627.

Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-being: Biodiversity Synthesis*. World Resources Institute, Washington, DC.

Milner-Gulland, E.J. & Mace, R. (1998) *Conservation of Biological Resources*. Blackwell Science, Oxford.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M. et al. (2001) What is the observed relationship between species richness and productivity? *Ecology*, 82, 2381–2396.

Moilanen, A., Smith, A.T. & Hanski, I. (1998) Long-term dynamics in a metapopulation of the American pika. *American Naturalist*, 152, 530–542.

Montagnes, D.J.S., Kimmance, S.A. & Atkinson, D. (2003) Using  $Q_{10}$ : can growth rates increase linearly with temperature? *Aquatic Microbial Ecology*, 32, 307–313.

Mosier, A.R., Bleken, M.A., Chaiwanakupt, P. et al. (2002) Policy implications of human-accelerated nitrogen cycling. *Biogeochemistry*, 57/58, 477–516.

Murdoch, W.W. (1966) Community structure, population control and competition – a critique. *American Naturalist*, 100, 219–226.

Murdoch, W.W. & Stewart-Oaten, A. (1975) Predation and population stability. *Advances in Ecological Research*, 9, 1–131.

Mwendera, E.J., Saleem, M.A.M. & Woldu, Z. (1997) Vegetation response to cattle grazing in the Ethiopian Highlands. *Agriculture, Ecosystems and Environment*, 64, 43–51.

Myers, R.A. (2001) Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. *ICES Journal of Marine Science*, 58, 937–951.

National Research Council (1990) *Alternative Agriculture*. National Academy of Sciences, Academy Press, Washington, DC.

Neilson, R.P., Prentice, I.C., Smith, B., Kittel, T. & Viner, D. (1998) Simulated changes in vegetation distribution under global warming. Available as Annex C at [www.epa.gov/globalwarming/reports/pubs/ipcc/annex/index.html](http://www.epa.gov/globalwarming/reports/pubs/ipcc/annex/index.html).

NERC (1990) *Our Changing Environment*. Natural Environment Research Council, London. (NERC acknowledges the significant contribution of Fred Pearce to the document.)

Newsham, K.K., Fitter, A.H. & Watkinson, A.R. (1994) Root pathogenic and arbuscular mycorrhizal mycorrhizal fungi determine fecundity of asymptomatic plants in the field. *Journal of Ecology*, 82, 805–814.

Newsham, K.K., Fitter, A.H. & Watkinson, A.R. (1995) Multi-functionality and biodiversity in arbuscular mycorrhizas. *Trends in Ecology and Evolution*, 10, 407–411.

Niklas, K.J., Tiffney, B.H. & Knoll, A.H. (1983) Patterns in vascular land plant diversification. *Nature*, 303, 614–616.

Nilsson, L.A. (1988) The evolution of flowers with deep corolla tubes. *Nature*, 334, 147–149.

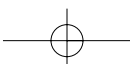
Norton, I.O. & Sclater, J.G. (1979) A model for the evolution of the Indian Ocean and the breakup of Gondwanaland. *Journal of Geophysical Research*, 84, 6803–6830.

Nowak, R.M. (1979) *North American Quaternary Canis*. Monograph No. 6, Museum of Natural History. University of Kansas, Lawrence, KA.

O'Brien, E.M. (1993) Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. *Journal of Biogeography*, 20, 181–198.

Oaks, J.L., Gilbert, M., Virani, M.Z. et al. (2004) Diclofenac residues as the cause of vulture population decline in Pakistan. *Nature*, 427, 629–633.

Oedekoven, M.A. & Joern, A. (2000) Plant quality and spider predation affects grasshoppers (Acrididae): food-quality-dependent compensatory mortality. *Ecology*, 81, 66–77.







Ogden, J. (1968) *Studies on reproductive strategy with particular reference to selected composites*. PhD thesis, University of Wales, Bangor.

Osmundson, D.B., Ryel, R.J., Lamarra, V.L. & Pitlick, J. (2002) Flow-sediment-biota relations: implications for river regulation effects on native fish abundance. *Ecological Applications*, 12, 1719–1739.

Owen-Smith, N. (1987) Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology*, 13, 351–362.

Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999) Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, 14, 483–488.

Paine, R.T. (1966) Food web complexity and species diversity. *American Naturalist*, 100, 65–75.

Paine, R.T. (1979) Disaster, catastrophe and local persistence of the sea palm *Postelsia palmaeformis*. *Science*, 205, 685–687.

Paterson, S. & Viney, M.E. (2002) Host immune responses are necessary for density dependence in nematode infections. *Parasitology*, 125, 283–292.

Pauly, D. & Christensen, V. (1995) Primary production required to sustain global fisheries. *Nature*, 374, 255–257.

Pavia, H. & Toth, G.B. (2000) Inducible chemical resistance to herbivory in the brown seaweed *Ascophyllum nodosum*. *Ecology*, 81, 3212–3225.

Pearl, R. (1927) The growth of populations. *Quarterly Review of Biology*, 2, 532–548.

Pearl, R. (1928) *The Rate of Living*. Knopf, New York.

Pearson, D.E. & Callaway, R.M. (2003) Indirect effects of host-specific biological control agents. *Trends in Ecology and Evolution*, 18, 456–461.

Penn, A.M., Sherwin, W.B., Gordon, G., Lunney, D., Melzer, A. & Lacy, R.C. (2000) Demographic forecasting in koala conservation. *Conservation Biology*, 14, 629–638.

Pennings, S.C. & Callaway, R.M. (2002) Parasitic plants: parallels and contrasts with herbivores. *Oecologia*, 131, 479–489.

Perrins, C.M. (1965) Population fluctuations and clutch size in the great tit, *Parus major* L. *Journal of Animal Ecology*, 34, 601–647.

Petren, K. & Case, T.J. (1996) An experimental demonstration of exploitation competition in an ongoing invasion. *Ecology*, 77, 118–132.

Petren, K., Grant, B.R. & Grant, P.R. (1999) A phylogeny of Darwin's finches based on microsatellite DNA variation. *Proceedings of the Royal Society of London, Series B*, 266, 321–329.

Pimentel, D. (1993) Cultural controls for insect pest management. In: *Pest Control and Sustainable Agriculture* (S. Corey, D. Dall & W. Milne, eds), pp. 35–38. Commonwealth Scientific and Research Organisation, East Melbourne, New South Wales.

Pimentel, D., Krummel, J., Gallahan, D. et al. (1978) Benefits and costs of pesticide use in U.S. food production. *Bioscience*, 28, 777–784.

Pimentel, D., Lach, L., Zuniga, R. & Morrison, D. (2000) Environmental and economic costs of nonindigenous species in the United States. *BioScience*, 50, 53–65.

Pimm, S.L. (1991) *The Balance of Nature: Ecological Issues in the Conservation of Species and Communities*. University of Chicago Press, Chicago.

Pitcher, T.J. & Hart, P.J.B. (1982) *Fisheries Ecology*. Croom Helm, London.

Pope, S.E., Fahrig, L. & Merriam, H.G. (2000) Landscape complementation and metapopulation effects on leopard frog populations. *Ecology*, 81, 2498–2508.

Power, M.E., Tilman, D., Estes, J.A. et al. (1996) Challenges in the quest for keystones. *Bioscience*, 46, 609–620.

Primack, R.B. (1993) *Essentials of Conservation Biology*. Sinauer Associates, Sunderland, MA.

Pywell, R.F., Bullock, J.M., Walker, K.J., Coulson, S.J., Gregory, S.J. & Stevenson, M.J. (2004) Facilitating grassland diversification using the hemiparasitic plant *Rhinanthus minor*. *Journal of Applied Ecology*, 41, 880–887.

Raffaelli, D. & Hawkins, S. (1996) *Intertidal Ecology*. Kluwer, Dordrecht.

Rahbek, C. (1995) The elevational gradient of species richness: a uniform pattern? *Ecography*, 18, 200–205.

Rainey, P.B. & Trevisano, M. (1998) Adaptive radiation in a heterogeneous environment. *Nature*, 394, 69–72.

Randall, M.G.M. (1982) The dynamics of an insect population throughout its altitudinal distribution: *Coleophora alticolella* (Lepidoptera) in northern England. *Journal of Animal Ecology*, 51, 993–1016.

Ratcliffe, D.A. (1970) Changes attributable to pesticides in egg breakage frequency and eggshell thickness in some British birds. *Journal of Applied Ecology*, 7, 67–107.

Rätti, O., Dufva, R. & Alatalo, R.V. (1993) Blood parasites and male fitness in the pied flycatcher. *Oecologia*, 96, 410–414.

Reganold, J.P., Glover, J.D., Andrews, P.K. & Hinman, H.R. (2001) Sustainability of three apple production systems. *Nature*, 410, 926–929.

Ribas, C.R., Schoereder, J.H., Pic, M. & Soares, S.M. (2003) Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. *Austral Ecology*, 28, 305–314.

Ricklefs, R.E. (1973) *Ecology*. Nelson, London.

Ricklefs, R.E. & Lovette, I.J. (1999) The role of island area *per se* and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology*, 68, 1142–1160.

Ridley, M. (1993) *Evolution*. Blackwell Science, Boston.

Riis, T. & Sand-Jensen, K. (1997) Growth reconstruction and photosynthesis of aquatic mosses: influence of light, temperature and carbon dioxide at depth. *Journal of Ecology*, 85, 359–372.

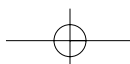
Risebrough, R. (2004) Fatal medicine for vultures. *Nature*, 427, 596–598.

Rodrigues, A.S.L., Pilgrim, J.D., Lamoreux, J.F., Hoffmann, M. & Brooks, T.M. (2006) The value of the IUCN Red List for conservation. *Trends in Ecology and Evolution*, 21, 71–76.

Rohr, D.H. (2001) Reproductive trade-offs in the elapid snakes *Austrelap superbus* and *Austrelap ramsayi*. *Canadian Journal of Zoology*, 79, 1030–1037.

Root, R. (1967) The niche exploitation pattern of the blue-grey gnatcatcher. *Ecological Monographs*, 37, 317–350.

Rosenthal, G.A., Dahlman, D.L. & Janzen, D.H. (1976) A novel means for dealing with L-canavanine, a toxic metabolite. *Science*, 192, 256–258.





Rosenzweig, M.L. (1971) Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science*, 171, 385–387.

Rosenzweig, M.L. & Sandlin, E.A. (1997) Species diversity and latitudes: listening to area's signal. *Oikos*, 80, 172–176.

Rouphael, A.B. & Inglis, G.J. (2001) 'Take only photographs and leave only footprints'? An experimental study of the impacts of underwater photographers on coral reef dive sites. *Biological Conservation*, 100, 281–287.

Roura-Pascual, N., Suarez, A.V., Gomez, C., Pons, P., Touyama, Y., Wild, A.L. & Townsend Peterson, A. (2004) Geographical potential of Argentine ants (*Linepithema humile* Mayr) in the face of global climate change. *Proceedings of the Royal Society of London, Series B*, 271, 2527–2534.

Rowe, C.L. (2002) Differences in maintenance energy expenditure by two estuarine shrimp (*Palaemonetes pugio* and *P. vulgaris*) that may permit partitioning of habitats by salinity. *Comparative Biochemistry and Physiology A*, 132, 341–351.

Roy, M.S., Geffen, E., Smith, D., Ostrander, E.A. & Wayne, R.K. (1994) Patterns of differentiation and hybridization in North American wolflike canids, revealed by analysis of microsatellite loci. *Molecular Biology and Evolution*, 11, 553–570.

Ruiters, C. & McKenzie, B. (1994) Seasonal allocation and efficiency patterns of biomass and resources in the perennial geophyte *Sparaxis grandiflora* subspecies *fimbriata* (Iridaceae) in lowland coastal Fynbos, South Africa. *Annals of Botany*, 74, 633–646.

Sale, P.F. (1979) Recruitment, loss and coexistence in a guild of territorial coral reef fishes. *Oecologia*, 42, 159–177.

Sale, P.F. & Douglas, W.A. (1984) Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. *Ecology*, 65, 409–422.

Salisbury, E.J. (1942) *The Reproductive Capacity of Plants*. Bell, London.

Sanders, N.J., Moss, J. & Wagner, D. (2003) Patterns of ant species richness along elevational gradients in an arid ecosystem. *Global Ecology and Biogeography*, 12, 93–102.

Santelmann, M.V., White, D., Freemark, K. et al. (2004) Assessing alternative futures for agriculture in Iowa, USA. *Landscape Ecology*, 19, 357–374.

Savidge, J.A. (1987) Extinction of an island forest avifauna by an introduced snake. *Ecology*, 68, 660–668.

Sax, D.F. & Gaines, S.D. (2003) Species diversity: from global decreases to local increases. *Trends in Ecology and Evolution*, 18, 561–566.

Schluter, D. (2001) Ecology and the origin of species. *Trends in Ecology and Evolution*, 16, 372–380.

Schoener, T.W. (1983) Field experiments on interspecific competition. *American Naturalist*, 122, 240–285.

Schoenly, K., Beaver, R.A. & Heumier, T.A. (1991) On the trophic relations of insects: a food-web approach. *American Naturalist*, 137, 597–638.

Schulze, E.D. (1970) Dre CO<sub>2</sub>-Gaswechsel de Buche (*Fagus sylvatica* L.) in Abhängigkeit von den Klimafaktoren in Freiland. *Flora, Jena*, 159, 177–232.

Schulze, E.D., Fuchs, M.I. & Fuchs, M. (1977a) Spatial distribution of photosynthetic capacity and performance in a mountain spruce forest in northern Germany. I. Biomass distribution and daily CO<sub>2</sub> uptake in different crown layers. *Oecologia*, 29, 43–61.

Schulze, E.D., Fuchs, M.I. & Fuchs, M. (1977b) Spatial distribution of photosynthetic capacity and performance in a mountain spruce forest in northern Germany. III. The significance of the evergreen habit. *Oecologia*, 30, 239–249.

Schwartz, O.A., Armitage, K.B. & Van Vuren, D. (1998) A 32-year demography of yellow-bellied marmots (*Marmota flaviventris*). *Journal of Zoology*, 246, 337–346.

Shankar Raman, T., Rawat, G.S. & Johnsingh, A.J.T. (1998) Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, north-east India. *Journal of Applied Ecology*, 35, 214–231.

Sibly, R.M. & Hone, J. (2002) Population growth rate and its determinants: an overview. *Philosophical Transactions of the Royal Society of London, Series B*, 357, 1153–1170.

Simberloff, D.S. (1976) Experimental zoogeography of islands: effects of island size. *Ecology*, 57, 629–648.

Simberloff, D.S., Dayan T., Jones, C. & Ogura, G. (2000) Character displacement and release in the small Indian mongoose, *Herpestes javanicus*. *Ecology*, 91, 2086–2099.

Simon, K.S., Townsend, C.R., Biggs, B.J.F., Bowden, W.B. & Frew, R.D. (2004) Habitat-specific nitrogen dynamics in New Zealand streams containing native or invasive fish. *Ecosystems*, 7, 777–792.

Sinclair, B.J. & Sjørnsen, H. (2001) Cold tolerance of the Antarctic springtail *Gomphiocephalus hodgsoni* (Collembola, Hypogastruridae). *Antarctic Science*, 13, 277–279.

Singleton, G., Krebs, C.J., Davis, S., Chambers, L. & Brown, P. (2001) Reproductive changes in fluctuating house mouse populations in southeastern Australia. *Proceedings of the Royal Society of London, Series B*, 268, 1741–1748.

Slobodkin, L.B., Smith, F.E. & Hairston, N.G. (1967) Regulation in terrestrial ecosystems, and the implied balance of nature. *American Naturalist*, 101, 109–124.

Smith, J.W. (1998) Boll weevil eradication: area-wide pest management. *Annals of the Entomological Society of America*, 91, 239–247.

Sousa, M.E. (1979a) Experimental investigation of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs*, 49, 227–254.

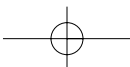
Sousa, M.E. (1979b) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*, 60, 1225–1239.

Stenseth, N.C., Falck, W., Bjørnstad, O.N. & Krebs, C.J. (1997) Population regulation in snowshoe hare and lynx populations: asymmetric food web configurations between the snowshoe hare and the lynx. *Proceedings of the National Academy of Science of the USA*, 94, 5147–5152.

Stevens, C.E. & Hume, I.D. (1998) Contributions of microbes in vertebrate gastrointestinal tract to production and conservation of nutrients. *Physiological Reviews*, 78, 393–426.

Stoll, P. & Prati, D. (2001) Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology*, 82, 319–327.

Strauss, S.Y. & Agrawal, A.A. (1999) The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution*, 14, 179–185.





Strauss, S.Y., Irwin, R.E. & Lambrix, V.M. (2004) Optimal defence theory and flower petal colour predict variation in the secondary chemistry of wild radish. *Journal of Ecology*, 92, 132–141.

Strong, D.R. Jr., Lawton, J.H. & Southwood, T.R.E. (1984) *Insects on Plants: Community Patterns and Mechanisms*. Blackwell Scientific Publications, Oxford.

Susarla, S., Medina, V.F. & McCutcheon, S.C. (2002) Phytoremediation: an ecological solution to organic chemical contamination. *Ecological Engineering*, 18, 647–658.

Sutherland, W.J., Gill, J.A. & Norris, K. (2002) Density-dependent dispersal in animals: concepts, evidence, mechanisms and consequences. In: *Dispersal Ecology* (J.M. Bullock, R.E. Kenward & R.S. Hails, eds), pp. 134–151. Blackwell Publishing, Oxford.

Sutton, S.L. & Collins, N.M. (1991) Insects and tropical forest conservation. In: *The Conservation of Insects and their Habitats* (N.M. Collins & J.A. Thomas, eds), pp. 405–424. Academic Press, London.

Swan, G., Naidoo, V., Cuthbert, R. et al. (2006) Removing the threat of diclofenac to critically endangered Asian vultures. *Public Library of Science Biology*, 4(3), e66. doi: 10.1371/journal.pbio.0040066.

Swift, M.J., Heal, O.W. & Anderson, J.M. (1979) *Decomposition in Terrestrial Ecosystems*. Blackwell Scientific Publications, Oxford.

Swinnerton, K.J., Groombridge, J.J., Jones, C.G., Burn, R.W. & Munroo, Y. (2004) Inbreeding depression and founder diversity among captive and free-living populations of the endangered pink pigeon *Columba mayeri*. *Animal Conservation*, 7, 353–364.

Symonides, E. (1979) The structure and population dynamics of psammophytes on inland dunes. II. Loose-sod populations. *Ekologia Polska*, 27, 191–234.

Symonides, E. (1983) Population size regulation as a result of intra-population interactions. I. The effect of density on the survival and development of individuals of *Erophila verna* (L.). *Ekologia Polska*, 31, 839–881.

Tanaka, M.O. & Magalhaes, C.A. (2002) Edge effects and succession dynamics in *Brachidontes* mussel beds. *Marine Ecology Progress Series*, 237, 151–158.

Taniguchi, Y. & Nakano, S. (2000) Condition-specific competition: implications for the altitudinal distribution of stream fishes. *Ecology*, 81, 2027–2039.

Tansley, A.G. (1904) The problems of ecology. *New Phytologist*, 3, 191–200.

Taylor, I. (1994) *Barn Owls. Predator–Prey Relationships and Conservation*. Cambridge University Press, Cambridge.

Téllez-Valdés, O. & Dávila-Aranda, P. (2003) Protected areas and climate change: a case study of the cacti in the Tehuacán-Cuicatlán Biosphere Reserve, Mexico. *Conservation Biology*, 17, 846–853.

Thomas, C.D., Cameron, A., Green, R.E. et al. (2004) Extinction risk from climate change. *Nature*, 427, 145–148.

Thomas, C.D. & Harrison, S. (1992) Spatial dynamics of a patchily distributed butterfly species. *Journal of Applied Ecology*, 61, 437–446.

Thomas, C.D. & Jones, T.M. (1993) Partial recovery of a skipper butterfly (*Hesperia comma*) from population refuges: lessons for conservation in a fragmented landscape. *Journal of Animal Ecology*, 62, 472–481.

Thomas, C.D., Thomas, J.A. & Warren, M.S. (1992) Distributions of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia*, 92, 563–567.

Thompson, R.M., Townsend, C.R., Craw, D., Frew, R. & Riley, R. (2001) (Further) links from rocks to plants. *Trends in Ecology and Evolution*, 16, 543.

Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.

Tilman, D. (1986) Resources, competition and the dynamics of plant communities. In: *Plant Ecology* (M.J. Crawley, ed.), pp. 51–74. Blackwell Scientific Publications, Oxford.

Tilman, D. (1996) Biodiversity: population versus ecosystem stability. *Ecology*, 77, 350–363.

Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, 80, 1455–1474.

Tilman, D., Fargione, J., Wolff, B. et al. (2001) Forecasting agriculturally driven global environmental change. *Science*, 292, 281–284.

Tilman, D., Mattson, M. & Langer, S. (1981) Competition and nutrient kinetics along a temperature gradient: an experimental test of a mechanistic approach to niche theory. *Limnology and Oceanography*, 26, 1020–1033.

Tokeshi, M. (1993) Species abundance patterns and community structure. *Advances in Ecological Research*, 24, 112–186.

Tonn, W.M. & Magnuson, J.J. (1982) Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology*, 63, 137–154.

Townsend, C.R. (2007) *Ecological Applications: Toward a Sustainable World*. Blackwell Publishing, Oxford.

Townsend, C.R. & Crowl, T.A. (1991) Fragmented population structure in a native New Zealand fish: an effect of introduced brown trout? *Oikos*, 61, 348–354.

Townsend, C.R., Hildrew, A.G. & Francis, J.E. (1983) Community structure in some southern English streams: the influence of physiochemical factors. *Freshwater Biology*, 13, 521–544.

Townsend, C.R., Scarsbrook, M.R. & Dolédec, S. (1997) The intermediate disturbance hypothesis, refugia and bio-diversity in streams. *Limnology and Oceanography*, 42, 938–949.

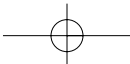
Townsend, C.R., Thompson, R.M., McIntosh, A.R. et al. (1998) Disturbance, resource supply, and food-web architecture in streams. *Ecology Letters*, 1, 200–209.

Turkington, R. & Harper, J.L. (1979) The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. IV. Fine scale biotic differentiation. *Journal of Ecology*, 67, 245–254.

Turner, J.R.G., Lennon, J.J. & Greenwood, J.J.D. (1996) Does climate cause the global biodiversity gradient? In: *Aspects of the Genesis and Maintenance of Biological Diversity* (M. Hochberg, J. Claubert & R. Barbault, eds), pp. 199–220. Oxford University Press, London.

UNEP (2003) *Global Environmental Outlook Year Book 2003*. United Nations Environmental Program (UNEP), GEO Section, Nairobi, Kenya.

United Nations (1998) *Global Change and Sustainable Development: Critical Trends*. Report of the Secretary General, United Nations, New York. (Also available on the world wide web at [www.un.org/esa/sustdev/trends.html](http://www.un.org/esa/sustdev/trends.html).)







United Nations (2002) *Global Environmental Outlook 3*. Report of the United Nations Environmental Program (UNEP). UNEP, [www.unep.org/GEO/geo3](http://www.unep.org/GEO/geo3).

United Nations (2005) *The World Population Prospects: the 2004 Revision*. Analytical Report Vol. III. Department of Economic and Social Affairs, Population Division, United Nations. United Nations, New York.

Valentine, J.W. (1970) How many marine invertebrate fossil species? A new approximation. *Journal of Paleontology*, 44, 410–415.

Valladares, V.F. & Pearcy, R.W. (1998) The functional ecology of shoot architecture in sun and shade plants of *Heteromeles arbutifolia* M. Roem., a Californian chaparral shrub. *Oecologia*, 114, 1–10.

van der Juegd, H.P. (1999) *Life history decisions in a changing environment: a long-term study of a temperate barnacle goose population*. PhD thesis, Uppsala University, Uppsala.

Vannotte, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushing, C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37, 130–137.

Vázquez, G.J.A. & Givnish, T.J. (1998) Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlán. *Journal of Ecology*, 86, 999–1020.

Verhoeven, J.T.A., Arheimer, B., Yin, C. & Hefting, M.M. (2006) Regional and global concerns over wetlands and water quality. *Trends in Ecology and Evolution*, 21, 96–103.

Volterra, V. (1926) Variations and fluctuations of the numbers of individuals in animal species living together. (Reprinted in 1931. In: *Animal Ecology* (R.N. Chapman, ed.), pp. 409–448. McGraw Hill, New York.)

Waage, J.K. & Greathead, D.J. (1988) Biological control: challenges and opportunities. *Philosophical Transactions of the Royal Society of London, Series B*, 318, 111–128.

Walsh, J.A. (1983) Selective primary health care: strategies for control of disease in the developing world. IV. Measles. *Reviews of Infectious Diseases*, 5, 330–340.

Wang, G.-H. (2002) Plant traits and soil chemical variables during a secondary vegetation succession in abandoned fields on the Loess Plateau. *Acta Botanica Sinica*, 44, 990–998.

Wardle, D.A., Bonner, K.I. & Barker, G.M. (2000) Stability of ecosystem properties in response to above-ground functional group richness and composition. *Oikos*, 89, 11–23.

Warren, P.H. (1989) Spatial and temporal variation in the structure of a freshwater food web. *Oikos*, 55, 299–311.

Watkinson, A.R. & Harper, J.L. (1978) The demography of a sand dune annual: *Vulpia fasciculata*. I. The natural regulation of populations. *Journal of Ecology*, 66, 15–33.

Wayne, R.K. (1996) Conservation genetics in the Canidae. In: *Conservation Genetics* (J.C. Avise & J.L. Hamrick, eds), pp. 75–118. Chapman & Hall, New York.

Wayne, R.K. & Jenks, S.M. (1991) Mitochondrial DNA analysis implying extensive hybridization of the endangered red wolf *Canis rufus*. *Nature*, 351, 565–568.

Webb, S.D. (1987) Community patterns in extinct terrestrial invertebrates. In: *Organization of Communities: Past and Present* (J.H.R. Gee & P.S. Giller, eds), pp. 439–468. Blackwell Scientific Publications, Oxford.

Webb, W.L., Lauenroth, W.K., Szarek, S.R. & Kinerson, R.S. (1983) Primary production and abiotic controls in forests, grasslands and desert ecosystems in the United States. *Ecology*, 64, 134–151.

Wegener, A. (1915) *Entstehung der Kontinenter und Ozeaner*. Samml. Viewig, Braunschweig. (English translation 1924. *The Origins of Continents and Oceans*, translated by J.G.A. Skerl. Methuen, London.)

White, G. (1789) *The Natural History and Antiquities of Selborne*. (Reprinted in 1977 as *The Natural History of Selborne* (G. White and R. Mabey). Penguin, London.)

Whitehead, A.N. (1953) *Science and the Modern World*. Cambridge University Press, Cambridge.

Whittaker, R.J., Willis, K.J. & Field, R. (2003) Climatic–energetic explanations of diversity: a macroscopic perspective. In: *Macroecology: Concepts and Consequences* (T.M. Blackburn & K.J. Gaston, eds), pp. 107–129. Blackwell Publishing, Oxford.

Williams, W.D. (1988) Limnological imbalances: an antipodean viewpoint. *Freshwater Biology*, 20, 407–420.

Winemiller, K.O. (1990) Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs*, 60, 331–367.

Withler, R.E., Candy, J.R., Beacham, T.D. & Miller, K.M. (2004) Forensic DNA analysis of Pacific salmonid samples for species and stock identification. *Environmental Biology of Fishes*, 69, 275–285.

Woiwod, I.P. & Hanski, I. (1992) Patterns of density dependence in moths and aphids. *Journal of Animal Ecology*, 61, 619–629.

Wolff, J.O., Schauber, E.M. & Edge, W.D. (1997) Effects of habitat loss and fragmentation on the behavior and demography of gray-tailed voles. *Conservation Biology*, 11, 945–956.

Wootton, J.T. (1992) Indirect effects, prey susceptibility, and habitat selection: impacts of birds on limpets and algae. *Ecology*, 73, 981–991.

Worland, M.R. & Convey, P. (2001) Rapid cold hardening in Antarctic microarthropods. *Functional Ecology*, 15, 515–524.

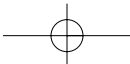
Wright, S., Keeling, J. & Gillman, L. (2006) The road from Santa Rosalia: a faster tempo of evolution in tropical climates. *Proceedings of the National Academy of Sciences of the USA*, 103, 7718–7722.

Yao, I., Shibao, H. & Akimoto, S. (2000) Costs and benefits of ant attendance to the drepanosiphid aphid *Tuberculatus quercicola*. *Oikos*, 89, 3–10.

Yodzis, P. (1986) Competition, mortality and community structure. In: *Community Ecology* (J. Diamond & T.J. Case, eds), pp. 480–491. Harper & Row, New York.

Yoshida, T., Jones, L.E., Ellner, S.P., Fussmann, G.F. & Hairston, N.G., Jr. (2003) Rapid evolution drives ecological dynamics in a predator–prey system. *Nature*, 424, 303–306.

Zimmer, M. & Topp, W. (2002) The role of coprophagy in nutrient release from feces of phytophagous insects. *Soil Biology and Biochemistry*, 34, 1093–1099.



# Index

## INDEX

Page numbers in *italic* refer to figures and/or tables separate from the text

- Abies balsamea* (balsam fir) 115  
 abundance  
   determination 285–7, 293  
   and dispersal 166–8  
   fluctuations 283, 284  
   indices of 150–1, 285  
   key factor analysis 287–94  
   observation of changes 10  
   oscillations/cycles 233–4, 235–6  
     coupled 234, 236–9  
   and predation 220–1, 233–4  
   regulation 285–7, 293  
   stability 284, 285  
 abundance index 285  
*Acacia burkittii* 162, 163  
*Acacia cornigera* (bull's horn acacia) 269–70  
*Accipiter nisus* (sparrow hawk) 425, 426  
 acclimatization/acclimation 76–7, 81  
*Acer saccharum* (sugar maple) 127  
 acid rain 28–9, 30, 426, 427, 438, 439, 461  
 acidic soils 115  
 acidophiles 84  
 acorn weevil 97  
*Actinia tenebrosa* 45  
 activated sludge method 444  
 adapting mosaic scenario 451, 452  
 adenine 254, 256  
 AE (assimilation efficiency) 366, 367  
*Aeschylanthus* 124  
 African ground squirrel 102  
 age as predictor of fecundity 156, 157  
 age-specific fecundity schedules 158  
 age structure 162, 163  
*Ageneotettix deorum* 226  
 agriculture  
   contour-based cultivation 409–10  
   and global climate change 419, 420, 421  
   and habitat degradation 428–35, 453  
   integrated farming systems 417–19  
   intensive cropping 429–30  
   intensive livestock management 428–9  
   and landscape management 449–50, 451  
   monocultures 405–11, 420–1  
   and mutualism 270–1  
   old-field succession 23–6, 34, 302, 303, 304  
   pest control 412–17  
   pollution due to 331, 379, 413, 425–6, 428–33, 453  
   and soil degradation and erosion 407–10, 424  
   sustainability 405–20  
*Agriolimnax reticulatus* 100  
*Agrostis capillaris* 50  
   cultivar 'Parys' 448  
*Agrostis stolonifera* (creeping bent grass) 43, 44  
*Ailuropoda melanoleuca* (giant panda) 459, 463  
*Aira praecox* 194, 195  
 Alabama leafworm 413  
 alder 117, 118, 371–2  
 aldrin 414  
 algae 136, 338, 430  
 alien species *see* invader species  
 alleles 256, 465  
 allelochemicals 424  
*Alnus incana* 371–2  
*Alnus sieboldiana* 117, 118  
 alternative energy sources 435  
 altitude  
   and biome distribution 114, 116  
   and lake characteristics 136, 137  
   and species richness 346–7  
 aluminum 438  
*Amblyseius californicus* 73  
 American pika (*Ochotona princeps*) 296–7  
 ammonium 376  
*Ammophila breviligulata* 302, 303  
*Amphiprion leucokranos* 202, 203  
*Amphiprion percula* 202, 203  
*Amphiprion perideraion* 202, 203  
*Amphiprion sandaracinos* 202, 203  
 AM (arbuscular mycorrhizal) fungi 274, 275–6  
 anaerobic conditions 130–1  
 analogous structures 63  
 anchovy (*Engraulis ringens*) 137, 402, 403  
*Androsace septentrionalis* 284, 285, 291, 292  
 anemone fish 202, 203  
 anemones 45, 202, 203  
 animals  
   body composition 96, 99  
   defenses 101–3  
   nutrition 96–9  
   resources 95–103, 108  
   and succession 305  
*Anisopteromalus calandrae* 245  
 annual plants 151  
   cohort life tables 158–61, 162  
   life cycle 153–4  
   in old-field succession 24, 25  
*Anolis* 56  
 Antarctic springtail 76–7  
 Antarctica 128  
*Anthoxanthum odoratum* 51  
*Antilocapra americana* (pronghorn antelope) 125, 126  
 ants  
   aphid farming 271  
   mutualisms with plants 269–70  
   species richness 329–30, 335  
   in trophic cascade 311, 312  
*Aphanes arvensis* 92  
 aphids 97, 99, 271  
*Apis mellifera* (honeybee) 97, 272, 433  
 aposematism 102  
 apple thrips 287  
 applied ecology 5, 34  
 aquaculture 405  
 aquatic environments 130–9, 140–1  
   cultural eutrophication 331, 379, 429–32, 443  
   detritivores 371  
   nutrient budgets 376, 378–9  
   patterns in conditions and resources 116–17  
   productivity 360, 363–4, 365  
   *see also* lakes; oceans; streams and rivers

- aquifers 411  
*Aquilegia* 273  
*Arabis fecunda* (sapphire rockcress) 42–3  
*Arachnothera* (sunbird) 124  
Arawak people 38  
arbuscular mycorrhizal fungi 274, 275–6  
Archaeobacteria 70, 74, 276  
Arctic 128, 477  
Arctic cod (*Gadus morhua*) 403–4, 434  
Arctic fox 84  
Arctic tern 83  
Argentine ant (*Linepithema humile*) 437, 438  
armadillo 102, 458  
‘arms race’ 262–3, 279  
insect–plant 263  
parasite–host 264–6, 267  
*Artemisia* 126  
*Artemisia gmelinii* 303  
*Artemisia scoparia* 303, 304  
*Artocarpus lanceifolius* 124  
*Ascaris* (roundworm) 39  
*Ascophyllum nodosum* 223–4  
Asian elephant (*Elephas maximus*) 253  
aspen (*Populus*) 127  
aspic viper (*Vipera aspis*) 176  
aspirin 458  
assimilation efficiency 366, 367  
*Asterionella formosa* 103, 183–4, 186–7  
atmosphere 375  
pollution 436–8, 439  
Australia, complementarity analysis of  
west coast 475  
autotrophs 95, 108  
average density 165–6  
avoiders 88–9  
*Azalea* 115
- bacteria 266, 267  
as decomposers 369, 370  
mutualistic role in digestion 273–4  
nitrogen fixation 276–8, 376, 429  
bacteriophage 266, 267  
*Balanus glandula* 332  
balsam fir (*Abies balsamea*) 115  
bamboo 156–7  
banana 407  
*Banksia dentata* 340  
*Banksia marginata* 340  
barbet (*Megalaima*) 124  
bark beetle 97  
barn owl 284  
barnacle 307, 308, 332  
barnacle goose (*Branta leucopsis*) 168  
basic reproductive rate 161, 240, 396–7  
Bates, H.W. 39  
*Beagle*, HMS 37, 38  
beech (*Fagus grandifolia*) 118  
beetles 343
- Beltian bodies 269, 270  
benthic animals 348  
*Betula* 76, 127  
*Betula nana* (dwarf birch) 207  
*Betula pendula* (silver birch) 169, 170  
*Betula pubescens* 76  
biennial plants 152  
bighorn sheep 464, 469  
bioclimatic law 80  
biodiversity 37, 456–9  
definition 456  
and disease 128  
history of the study of 38  
hotspots 474  
importance in ecosystem functioning  
372–3  
and landscape management 449–50,  
451  
and limiting resources 200–2  
Simpson’s index 200–1  
threats to 459–68, 480  
in tropical rain forests 122–4  
value of 457–8  
see also species richness  
biogeochemical cycles  
global 380–3, 384  
human impacts on 383  
biological control  
of pests 6, 415–17, 457–8  
of pollution 430  
biological scale 8  
biomagnification 433, 434  
biomanipulation 430, 431  
biomass 358  
biomes 113, 140  
description and classification 119,  
120–1, 122  
effects of altitude and latitude on  
distribution 114, 116  
lack of homogeneity 113–14  
predicted changes in distribution due  
to global climate change 128,  
129–30  
world distribution 114  
biospecies 52, 66  
birch (*Betula*) 76, 127, 169, 170, 207  
birds  
eggshell thickness 425–6  
extinctions 464, 467–8  
flightless 62–3  
and wind farms 441  
birth 146, 151, 152  
birth rate 147  
density-dependent/density-independent  
169, 170, 286  
human population 395, 396–7  
representation 170  
bison (*Bison bison*) 125, 126  
*Biston betularia* (peppered moth) 49–50
- black bear (*Ursus americanus*) 232, 233  
black-browed albatross (*Thalassarche*)  
256, 257, 258  
Black Death 393  
black guillemot (*Cepphus grylle*) 434  
black long-snouted weevil (*Cyrtobagus*)  
221  
black rockfish (*Sebastes melanops*) 405  
black-throated diver (*Gavia arctica*) 441  
blackfly (*Simulium vittatum*) 168  
blue tit (*Parus caeruleus*) 187  
bluebell (*Hyacinthoides non-scripta*)  
275–6  
bluejay 101, 102  
*Boiga irregularis* (brown tree snake)  
461–2  
boll weevil 413  
boreal coniferous forest see northern  
coniferous forest  
*Boreogadus saida* (polar cod) 434  
botanical gardens 38  
*Bothriochloa insculpta* 247  
*Bothriochloa ischaemum* 303, 304  
*Brachidontes darwinianus* 307, 308  
*Brachidontes solisianus* 307, 308  
*Brachysira vitrea* 439  
*Bracionus calyciflorus* 237  
*Branta leucopsis* (barnacle goose) 168  
brine shrimp 153  
British Isles  
effects of Chernobyl disaster 440  
invader species 352–3  
brook stickleback (*Culaea inconstans*)  
199  
brown bear (*Ursus arctos*) 232, 233  
brown tree snake (*Boiga irregularis*)  
461–2  
brown trout (*Salmo trutta*) 17–21, 34,  
131  
*Buceros rhinoceros* (hornbill) 124  
bulbul (*Chloropsis*) 124  
bull’s horn acacia (*Acacia cornigera*)  
269–70  
butterflies, risk of extinction 478
- cabbage root fly 101  
cacti 126  
biological control of pests 417  
risk of extinction 478–9  
and temperature extremes 74–5  
*Cactoblastis* 417  
calcium 91  
and acid rain 29  
in lakes 137  
in soil 115  
sources 375  
calling rank 151  
*Callosciurus nigrovittatus* (forest squirrel)  
124

- Callosobruchus chinensis* 245  
*Camarhynchus pallida* 54, 55  
*Camarhynchus psittacula* 54, 55  
 Cambrian explosion 349  
*Camnula pellucida* 78, 79  
 Canada lynx (*Lynx canadensis*) 236–8  
 Canary Islands 343  
 L-canavanine 263  
*Canis latrans* (coyote) 260, 261  
*Canis lupus* (gray wolf) 260, 261  
*Canis rufus* (red wolf) 260, 261, 262  
 Cape sugarbird (*Promerops cafer*) 272  
*Capsella bursa-pastoris* 194–5, 196  
 carbon 375  
   carbon cycle 381, 383  
   global budget 436  
   in nutritional resources 98–9  
   in oceans 378  
   sources 375  
   in terrestrial ecosystems 377  
 carbon dioxide 92–5, 375  
   atmospheric concentrations 92, 94, 436  
   from fossil fuel burning 436–7  
   and global climate change 93–4, 129  
   as pollutant 426  
   and productivity 360, 361  
   sequestration 427  
*Carcinus maenas* 247–8  
*Cardamine hirsuta* 195, 196  
 cardiac glycosides 101  
*Carex bigelowii* 207  
 caribou 128  
*Caring for the Earth: a Strategy for Sustainable Living* 390–1  
 carnivores 98–9  
   feces 373  
   invertebrate 134  
 carp 22  
 carrion consumption 373–4  
 carrying capacity 169–71, 172  
   global, human population 398–9, 420  
   and population dynamics 288  
*Caryedes brasiliensis* 263  
 cassowary 62  
*Castanopsis sieboldii* 117, 118  
 cat, feral 309, 310  
 catchment areas  
   Hubbard Brook experimental forest 27–30  
   management 449–50, 451  
*Catharanthus roseus* (rose periwinkle) 458  
 Cavendish banana 407  
 CE (consumption efficiency) 366–7  
 cecum 98  
 Cedar Creek Natural History Area 23–6, 34, 302, 317  
 cellulases 371  
 cellulolytic microbes 98  
 cellulose 97, 99, 273–4, 369, 371  
*Centaurea solstitialis* (yellow star thistle) 22, 23  
*Cephus grylle* (black guillemot) 434  
 cerrado 125  
*Certhidea olivacea* 54, 55, 56  
 CFCs 129, 437, 444–6  
*Chamaecrista fasciculata* 43–4  
 chaparral 114, 119  
 character displacement 198  
 characteristics, conservative 41  
 cheat grass 208–9  
 checkerboard score 214  
 chemosynthetic organisms 70  
*Chen caerulescens caerulescens* (lesser snow goose) 315  
*Chenopodium album* 153  
 Chernobyl 439–40  
 Cherokee darter (*Etheostoma scotti*) 134–5  
 chilling injury 74  
 China, effects of agriculture 408  
 chlordanes 434  
*Chlorella vulgaris* 237  
 chlorofluorocarbons (CFCs) 129, 437, 444–6  
 chlorophyll biomass 363  
*Chloropsis* (bulbul) 124  
 cholera 442  
*Chondrus crispus* 247–8  
*Choristoneura fumiferana* (spruce budworm) 128  
*Chorthippus brunneus* (common field grasshopper) 153  
 chronosequence 302  
*Chthamalus bisinuatus* 307, 308  
 cinnabar moth 96  
*Citrullus lanatus* (watermelon) 433  
 classical biological control 415–16  
 classification  
   community 131–2  
   taxonomic 131  
 Clean Air Act (USA) 29  
 cleaner fish 268, 269  
*Clematis javana* 340  
*Clematis paniculata* 340  
 Clements, F.E. 5  
 climate  
   and evolution 59–60, 66  
   instability and species richness 337  
   large-scale patterns 111–13  
   and latitude 346  
   small-scale patterns 114, 116  
   variations in and species richness 337–8, 354  
   see also global climate change  
 climax community 301, 306–7  
 cline 53  
 coal tit (*Parus ater*) 187, 246  
 coastal environments 138–9, 141, 475  
   rocky shore communities 331–2, 338, 339  
 cod  
   Atlantic Ocean fisheries 403–4  
   and pesticide use 434  
 coevolution 51, 252, 262–3, 279  
   insects and plants 263, 351  
   parasites and hosts 264–6, 267  
 coexistence  
   exploiter-mediated 333–4, 349  
   and interspecific competition 187–9, 192–3, 193–6, 196, 200–7  
   predator-mediated 246, 331–4  
 coho salmon (*Oncorhynchus kisutch*) 259  
 cohort 157  
 cohort life table 157–8, 158–61, 162  
*Coleophora alticola* (rush moth) 78  
 collector–filterers 371  
*Collisella subrugosa* 307, 308  
 colonization  
   in dominance-controlled communities 301  
   of islands 341–2, 344  
   and metapopulation dynamics 295–9  
   and population dynamics 288  
 Colorado beetle (*Leptinotarsa decemlineata*) 73, 166–7, 288–91  
 Colorado River, water abstraction 434–5  
*Columba mayeri* (pink pigeon) 472–3  
*Commidendrum robustum* (St Helena gumwood) 415–16  
 common field grasshopper (*Chorthippus brunneus*) 153  
 common garden experiments 42–4  
 communities 8, 34  
   cascading effects 20, 34  
   climax 301, 306–7  
   complexity 315–20  
   dominance-controlled 299, 301, 338  
   founder-controlled 299–301  
   homogenization 22, 462  
   resilient 314  
   resistant 314  
   stability  
     and food webs 313–20  
     fragile/robust 314  
     see also species richness; succession  
   community classification 131–2  
   community matrix 282  
   community structure  
     and interspecific competition 200–7, 215  
   neutral models and null hypotheses 211–14  
   and predation 246–8, 249  
   temporal patterns 299–307, 321

- competition 70  
 between predators 241–3  
 contest-like 105, 106  
 density-dependent 104, 167, 168, 169, 170, 241  
 exactly compensating 105–6  
 and dispersal 167, 168  
 in dominance-controlled communities 301  
 effects on resources 103–6, 108  
 exploitation 103, 183–4, 215  
 influence of conditions on 78, 80  
 interference 103  
 interspecific 183  
 between guilds 188–9  
 and coexistence 187–9, 192–3, 193–6, 196, 200–7  
 and community structure 200–7, 215  
 diffuse 188  
 ecological effects 183–95, 196, 215  
 and environmental heterogeneity 193–5, 196  
 evolutionary effects 197–9, 200, 215  
 impact on populations 173–4  
 Lotka–Volterra model 189, 190–2  
 neutral model approach 211–14  
 prevalence in current communities 209–11  
 significance in practice 208–14, 216  
 and species richness 327  
 surveys of field experiments 209–11  
 intraspecific 103–6, 108  
 impact on populations 169–75, 173–5, 180  
 and niche differentiation 199, 200  
 and parasitism 222, 242  
 competition coefficient 190  
 competitive exclusion  
 circumventing 333–4  
 Competitive Exclusion Principle 189, 192–3, 215  
 in founder-controlled communities 299  
 on islands 342  
 and predation 246  
 ‘competitive lottery’ 299  
 complementarity 372  
 complementarity analysis 475  
 conditions 107–8  
 descriptions of 71  
 distinction from resources 70  
 effects of 71–2, 73, 74–5  
 effects on disease 78, 79  
 effects on interactions between organisms 78, 79, 80  
 extreme 71, 72, 74–5, 83, 84, 107–8, 335–7, 354  
 and niche differentiation 204  
 patterns  
 aquatic environments 116–17  
 large-scale 111–13  
 small-scale 113–16  
 temporal 117, 118  
 response curves 71–2, 107  
 responses of animals 81–3, 84  
 responses of sedentary organisms 78, 80, 81  
 as stimuli 75–7  
 confidence intervals 14–15, 16  
*Connochaetes taurinus* (wildebeest) 125, 284  
 conservation 6, 456–9  
 and global climate change 476–9  
 in practice 468–76  
 and threats to biodiversity 459–68, 480  
 triage approach to priority setting 479  
 conservation areas, selection of 473–6, 481  
 conservation biological control 416  
 conservative characteristics 41  
 consumption efficiency 366–7  
 continental drift 60–3, 66  
 contingent valuation 428  
 contour-based cultivation 409–10  
 copper 91, 446–8  
 coral reefs 299–301, 461  
 corals 149  
 correlations 24, 283, 284  
 cotton, pests of 413–14  
 cotton aphid 413–14  
 cotton bollworm 413–14  
 cottongrass (*Eriophorum vaginatum*) 207  
 cottony cushion scale insect (*Icerya purchasi*) 415  
 covariance 47  
 cowries 101  
 coyote (*Canis latrans*) 260, 261  
 cranberry (*Vaccinium vitis-idaea*) 207  
*Crangon septemspinosa* (sand shrimp) 107  
 creeping bent grass (*Agrostis stolonifera*) 43, 44  
 creosote plant (*Larrea mexicana*) 126, 208  
 crested tit (*Parus cristatus*) 246  
 critically endangered species 459  
 crowding and predation 241–3  
 crypsis 102  
*Cryptochaetum* 415  
*Cryptopygus antarcticus* 76  
*Culaea inconstans* (brook stickleback) 199  
 cultural ecosystem services 427, 428, 458  
*Cuscuta salina* (dodder) 222  
 cyanogenic plants 100  
*Cyclotella meneghiniana* 186–7  
*Cymbella perpusilla* 439  
*Cynodon dactylon* 247  
*Cynometra inaequifolia* 124  
*Cyrtobagus* (black long-snouted weevil) 221  
 cysts 153  
 cytosine 254, 256  
 dams 410–11  
*Daphnia galeata mendotae* 430  
*Daphnia magna* 105  
*Daphnia pulicaria* 430, 431  
 Darwin, Charles 37–41, 39, 51, 52, 65, 273  
 Darwin’s finches 54, 55, 56, 198, 364  
*Dasypus novemcinctus* (nine-banded armadillo) 458  
 data-less management 405  
 DDT 146–7, 414, 425  
 death 146, 151, 152  
 death rate  
 density-dependent/density-independent 169, 170, 286  
 human population 395, 396–7  
 representation 170  
 decomposer system 359  
 energy flow through 366  
 relative role 367–9  
 decomposers 95, 99, 359, 364, 365, 369, 370, 374  
 interaction with detritivores 373  
 decomposition 369–74, 383–4  
 deep sea vents 57, 138  
 defenses 99–103  
 and coevolution 262–3  
 constitutive/inducible 100–1  
 plants 99–101, 126, 223–4, 262–3  
 definitions of ecology 4, 8, 34  
 deforestation 427–8  
 and atmospheric carbon dioxide levels 437  
 and biodiversity 461  
 effect on hydrological cycle 380–1  
 Hubbard Brook experimental forest 27–8, 29  
 and soil erosion 410  
 dehydration 74  
*Deinacrida mahoenuiensis* (weta) 306  
*Deleatidium* 18  
 demographic transition 395, 420  
 density-dependent processes  
 birth rate 169, 170, 286  
 competition 104, 105–6, 167, 168, 169, 170, 241  
 death rate 169, 170, 286  
 dispersal 167, 168  
 exactly compensating 105–6  
 and population regulation 286–7  
 depth, and species richness 347–8  
 descriptive studies 7



- desert 112, 114, 119, 120, 126, 140  
 creation 410, 424  
 ephemeral 'annual' species 153–4  
 invader species 208–9  
 plants 89–90, 92, 126  
 polar 128  
 productivity 361  
 rainfall 126, 153–4
- desert honeysweet (*Tidestromia oblongifolia*) 89–90
- desertization 410, 424
- detritivores 219, 359, 370–1  
 consumption of carrion 374  
 consumption of plant detritus 371–3  
 interaction with decomposers 373
- development, effects of temperature 72, 73, 74
- diapause 75–6
- diatoms 103, 183–4, 439
- dichlorodiphenyltrichloroethane (DDT) 146–7, 414, 425
- diclofenac poisoning 31–3, 35
- dieldrin 414, 432
- diet width 231–2
- differential equations 173
- digestive tracts  
 herbivores 98  
 mutualistic inhabitants 273–4  
 termites 8, 9
- Dioclea metacarpa* 262–3
- Dioscorides 38
- diphtheria 241
- disasters  
 Chernobyl 440  
 'dust bowl' 408  
 and population dynamics 288
- disease  
 and diversity 128  
 dynamics and cycles 240–1  
 as limiting factor in human population growth 399  
 in monocultures 406  
 response to conditions 78, 79
- dispersal 165–6, 180  
 and abundance 166–8  
 density dependent 167, 168  
 distance 294  
 inverse density dependence 167–8  
 and metapopulation dynamics 294–9  
 and population dynamics 294, 321  
 and predation 243–4
- dispersion *see* spatial distribution patterns
- display efficiency 88
- disturbance 282  
 and biodiversity 461  
 and community stability 317–20  
 and gap creation 299–301  
 intermediate disturbance hypothesis 338
- predation as 246  
 soil 153  
 and species richness 338–9, 354–5  
 streambed 132–3, 338–9
- diversity indices 324–5
- DNA 254  
 microsatellite 56, 255, 256, 257, 258, 260, 261  
 mitochondrial 255, 257, 258, 260, 261  
 mutation 254–5  
 nuclear 255  
 sequencing 255
- Dobzhansky, Theodosius 52, 252
- dodder (*Cuscuta salina*) 222
- Dolly Varden charr (*Salvelinus malma*) 78, 80, 184–6
- Doris* 39
- dormancy 75–6, 153–4
- Douglas fir (*Pseudotsuga menziesii*) 176, 226, 227, 335
- Dreissena polymorpha* (zebra mussel) 22, 23
- Dromaius novaehollandiae* (emu) 62, 63
- Drosophila* (fruitfly) 176, 345
- drought 88–9  
 desert 126  
 savanna 125
- dryfall 376
- duckweed (*Lemna*) 148
- dung beetles 373, 374
- 'dust bowl' disasters 408
- dwarf birch (*Betula nana*) 207
- dwarf willow (*Salix herbacea*) 344
- eastern hemlock (*Tsuga canadensis*) 115
- eastern white pine (*Pinus strobes*) 118, 303
- Echinocereus engelmannii* 92
- ECM fungi *see* ectomycorrhizal fungi
- ecological economics 457–8
- ecological energetics 358, 359
- ecological footprint 398
- economic injury levels 412–13, 417
- economic threshold 413
- ecosystem 8, 34  
 definition 358  
 importance of biodiversity in functioning 372–3
- ecosystem services  
 and biodiversity 457  
 cultural 427, 428, 458  
 effects of human activities 427–8  
 maintenance and restoration 448–51, 452, 454  
 provisioning 427, 428, 433, 458  
 regulating 427, 458  
 supporting 427
- ecotourism 458, 461
- ecotypes 448
- ectomycorrhizal (ECM) fungi 274–5  
 spatial separation 204, 206
- ectothermy 81–2, 367
- effective population size 466
- Eichhornia paniculata* 298–9
- EILs (economic injury levels) 412–13, 417
- El Niño events 403, 437
- Elephas maximus* (Asian elephant) 253
- Elton, Charles 5, 6
- emu (*Dromaius novaehollandiae*) 62, 63
- Encarsia formosa* 416
- endangered species 425, 459, 480
- Endangered Species Act (USA) 135
- endemic communities, effects of introduced species 462
- endothermy 81–3, 367
- endrin 414
- energy, alternative sources 435
- energy flux 358–69, 383  
 and trophic level 364–5, 366
- energy intake  
 net rate of 229, 230–1  
 and optimal diet width 231–2
- energy resources 410
- energy transfer efficiencies 365–7
- Engraulis ringens* (anchovy) 137, 402, 403
- Enteromorpha intestinalis* 247–8
- Entomophaga grylli* 79
- environmental conditions *see* conditions
- Eochonetes clarksvillensis* 214
- Eotetranychus sexmaculatus* 243–4
- epilimnion 135
- equilibrium abundance 412
- equilibrium theory of island biogeography 295, 341–2, 355, 474–5
- Equus burchellii* (zebra) 125
- Eriophorum vaginatum* (cottongrass) 207
- Erodium cicutarium* 194, 195
- Erophila verna* 164
- Esox lucius* (pike) 131, 430, 431
- estimation 15–16  
 from representative samples 150  
 indices of abundance 150–1  
 mark–recapture methods 150
- estuaries 139, 141
- ET (economic threshold) 413
- Etheostoma scotti* (Cherokee darter) 134–5
- Eucalyptus* 119, 126
- Eucalyptus coccifera* 340
- Eucalyptus deglupta* 340
- euphotic zone 136, 138, 364
- Eupomacentrus apicalis* 299–300
- European ground squirrel (*Spermophilus citellus*) 82
- eutrophication, cultural 331, 379, 429–32, 443
- evidence, diversity of 9–11, 34



- evolution 252
  - and climatic change 59–60, 66
  - and continental drift 60–3, 66
  - convergent 63, 66
  - definition 40
  - differing rates 340, 346
  - and interspecific competition 197–9, 200
  - on islands 344–5
  - and molecular ecology 253–62
  - by natural selection 37–41
  - parallel 63, 64, 66, 119
  - within species 41–51
- evolutionary ecology 252
- exactly compensating density-dependence 105–6
- exotic species *see* invader species
- experiments
  - common garden 42–4
  - laboratory 10, 34
  - manipulative field 10, 24–6, 34
  - natural 24
  - reciprocal transplant 42, 44–6
- exploitation 103, 183–4
  - effects on population dynamics 400–5
  - of natural resources 399–405, 420
- exploiter-mediated coexistence 333–4, 349
- extinction
  - chain of 465
  - drivers of 466–8
  - and fossil record 351–2, 456
  - and global climate change 476–9
  - and habitat area 463–4
  - and habitat fragmentation 464
  - hotspots 474
  - on islands 341–2, 464
  - and metapopulation dynamics 295–9
  - rate of 456–7
  - risk of 459–60, 466–8
  - in small populations 463–6, 467
- extinction vortex 468
- extreme conditions 71, 72, 74–5, 83, 84, 107–8, 335–7, 354
- Exxon Valdez* 446
- Fagus grandifolia* (beech) 118
- fairy bluebird (*Irena puella*) 124
- Falco peregrinus* (peregrine falcon) 425, 460
- false pink bollworm 413–14
- feces
  - consumption 373–4
  - disposal of 442–4
- fecundity
  - estimation 160–1
  - and predation 220–1
  - relationship with age and size 156, 157
- fecundity schedules 160, 179
  - age-specific 158
- fertilizers
  - controlled-release 429
  - and cultural eutrophication 331, 379, 429–32
  - minimization of losses 429
  - and pollution 426, 429
  - projected increase in use 420
  - sewage sludge as 444
  - and soil degradation 409
  - and species diversity 325, 326, 330–1, 333
- Festuca rubra* cultivar ‘Merlin’ 448
- Ficedula hypoleuca* (pied flycatcher) 220–1
- Ficus* 155
  - Ficus glabella* 124
  - Ficus rubinervis* 124
  - Ficus sumatrana* 124
- field experiments, manipulative 10, 24–6, 34
- field gentian (*Gentianella campestris*) 223, 224
- fire
  - and nutrient loss 377
  - role in savanna 125
- fish, species richness 330
- fisheries
  - aquaculture 405
  - maximum sustainable yields 399–405, 420
- fitness 40
  - and predation 220–1
- fixed effort harvesting 402–3
- fixed quota harvesting 401–2
- flamingo 136, 378
- flea beetle 220
- floodplains 133
- flowering, synchronous 157
- flying fox (*Pteropus*) 465
- food chains 359
- food origin, forensic analysis 258–9
- food webs 307–20, 321, 359
  - bottom-up control 312–13, 430
  - connectance 315, 316–17
  - decomposer 370
  - direct and indirect effects 309–13
  - interaction strength 315, 316–17
  - keystone species 314–15, 318
  - mathematical models 315–16
  - northern coniferous forest 237–8
  - and population/community stability 313–20
  - structure 313–20
  - top-down control 312–13, 430
  - trophic cascade 309–12
- foraging 228–33, 249
- forensic analysis of food origin 258–9
- forest
  - carbon dioxide concentrations 94–5
  - distribution of ectomycorrhizal fungi in pine forest 204, 206
  - energy flow pattern 368
  - experimental deciduous 26–30, 34–5
  - postglacial changes 58, 59, 60, 117, 118, 127–8
  - productivity 360
  - see also specific types*
- forest squirrel (*Callosciurus nigrovittatus*) 124
- forest tent caterpillar 239
- Formica yessensis* 271
- fossil fuels 435
  - and atmospheric pollution 436–8, 439
  - mining 446
- fossil record
  - and extinction 351–2, 456
  - taxon richness patterns 349–52, 355
- Fragaria* (strawberry) 149
- Fragilaria virescens* 439
- frost hardening 77
- fruitfly (*Drosophila*) 176, 345
- Frustulia rhomboides* 439
- fungi as decomposers 369, 370
- fur, seasonal changes in 83, 84
- Fusarium oxysporum* 275, 276
- Gadus morhua* (Arctic cod) 403–4, 434
- Galapagos Islands 54, 55, 56
- Galaxias* 17–21, 34
- gaps 299
  - and climax communities 307, 308
  - and dominance-controlled communities 301
  - and founder-controlled communities 299–301
  - primary succession 301–2
  - see also patches/patchiness*
- Gause’s (Competitive Exclusion) Principle 189, 192–3, 215
- Gavia arctica* (black-throated diver) 441
- gecko 184
- Gelidium coulteri* 338
- generations, length of 151
- genet 147
- genetic diversity
  - determinants of 466
  - in small populations 465–6, 467
- genetic drift 254
  - and genetic variation 466
- Gentianella campestris* (field gentian) 223, 224
- Gentianella germanica* 465–6, 467, 468
- Geospiza* 198
- Geospiza fortis* 54, 55, 364
- Geospiza fuliginosa* 54, 55
- Geospiza scandens* 54, 55

- giant panda (*Ailuropoda melanoleuca*) 459, 463
- gibbon (*Hylobates*) 124
- Gigartina canaliculata* 338
- Gigartina leptorhynchus* 338
- glacial cycles 58–60, 117, 118, 339–40
- Glanville fritillary butterfly (*Melitaea cinxia*) 296
- Glaucidium passerinum* (pigmy owl) 246
- glaucous gull (*Larus hyperboreus*) 434
- glaucous-winged gull (*Larus glaucescens*) 309–11
- global climate change 60, 80, 93–4, 437
- and conservation 476–9
- forecasting agriculturally driven 419, 420, 421
- predicted changes in biome distribution 128, 129–30
- and productivity 359
- global ecosystem 8
- global orchestration scenario 451, 452
- globalization 22
- Glomus* 275, 276
- glucosinolates 101
- Glycine soja* (soybean) 277–8
- Gomphiocephalus hodgsoni* 77
- goose barnacle (*Pollicipes polymerus*) 310–11
- gopher (*Thomomys bottae*) 125
- gorse (*Ulex europaeus*) 306
- GPP (gross primary productivity) 358, 363
- grasses as invader species 208–9
- grasshopper 78, 79, 97, 125, 153, 226
- grassland
- cultivated 126
- energy flow pattern 368
- restoration 333–4
- gray-tailed vole (*Microtus canicaudus*) 168
- gray wolf (*Canis lupus*) 260, 261
- grazers 95, 249
- and community structure 246–7
- compensation and defense responses to 223–5
- effects of invader species 20, 21
- effects on fitness and abundance 220, 221
- foraging 228, 249
- interacting factors adding to effects 222–3
- as predators 218, 219
- Great Barrier Reef 299–301, 461
- great tit (*Parus major*) 154–5, 156, 166, 187
- greater prairie chicken (*Tympanuchus cupido pinnatus*) 466
- greenhouse effect 437
- greenhouse gases 93, 129, 437, 444
- grey-headed albatross (*Thalassarche chrysostoma*) 256, 257, 258
- Gros Michel banana 407
- gross primary productivity 358, 363
- ground squirrel 243
- growth
- and cost of reproduction 151–2, 175, 176
- effects of temperature 72, 73, 74
- as life cycle stage 151–2
- guanine 254, 256
- guilds 188–9, 202
- Gulf Stream 112
- guppy (*Poecilia reticulata*) 46–7, 48
- Gutierrezia microcephala* 92
- Gyps bengalensis* (oriental white-backed vulture) 30–3
- Gyps indicus* (long-billed vulture) 30–3
- habitable sites and dispersal distance 294
- habitat 106
- area
- and risk of extinction 463–4
- and species richness 340–5, 355
- degradation 423–8
- due to agriculture 428–35, 453
- due to power generation 435–41, 453
- triple bottom-line approach to restoration 448–51, 452
- urban and industrial landscapes 442–8, 453–4
- disruption 460–1
- fragmentation 464–5
- Haeckel, Ernst 4
- Haematopus bachmani* (oystercatcher) 309–11
- halibut (*Hippoglossus stenolepis*) 403
- Haplopappus venetus* 226
- Hawaii 345
- hawkmoth 97
- heath hen (*Tympanuchus cupido cupido*) 463
- heavy metals 336
- hedgehog 102
- Helisoma trivolvis* 313
- Helminthosporium maydis* (southern corn leaf blight) 406
- Hemidactylus frenatus* 184
- Hemigymnus melapterus* 268, 269
- herbivores 96, 97–9, 101, 108
- ‘arms race’ with plants 263
- compensatory plant responses to 223–5, 262–3, 313
- digestive tracts 98
- feces 373
- in food webs 312–13
- generalist 263
- interspecific competition in 210–11
- oligophages 263
- savanna 125
- secondary productivity 364–5
- specialist 263
- tropical rain forests 123, 124
- Herpestes edwardsii* 197–8
- Herpestes javanicus* 197–8
- Herpestes smithii* 197–8
- herring gull (*Larus argentatus*) 53, 54
- Hesperia comma* (silver-spotted skipper butterfly) 297
- Heteractis crispa* 203
- Heteractis magnifica* 202, 203
- Heteromeles arbutifolia* 87–8
- heterotrophs 95, 108
- hibernation 82, 83
- Hippoglossus stenolepis* (halibut) 403
- Hirundo rustica* (swallow) 169
- historical aspects 5–7
- HIV infection 22
- homologous structures 63
- homozygosity 465
- honeybee (*Apis mellifera*) 97, 272, 433
- honeydew 99
- Hopkin’s bioclimatic law 80
- hornbill (*Buceros rhinoceros*) 124
- host 218
- coevolution with parasite 264–6, 267
- host races 53
- house mouse (*Mus domesticus*) 284, 285
- Hubbard Brook experimental forest 26–30, 34–5
- human activities
- economic costs 427–8
- effects on stream ecosystems 133, 134–5
- harvesting resources from the wild 399–405
- and loss of ecosystem services 427–8
- physical and chemical impacts 424–6
- and sustainability 389–421
- threats to biodiversity 460–2
- waste disposal 442–4
- human population 420
- age structure 392, 396, 397
- demographic transition 395, 420
- geographic distribution 392, 396
- global carrying capacity 398–9, 420
- growth
- future predictions 394–7
- and sustainability 392–3
- up to the present 291–4
- medium fertility variant 397
- and resource distribution 393
- zero growth 396
- humans
- average density in the USA 166
- migration and extinctions 351–2
- reproduction 155
- Humboldt current 112
- hunter-gatherers 405, 406

- Hyacinthoides non-scripta* (bluebell) 275–6
- hybrids 260, 261, 262
- Hydra* 148
- hydrogen cyanide 100
- hydrological cycle 380–1
- hydropower schemes 435, 440–1
- hydrosphere 375
- hydrothermal vents 57, 138
- Hylobates* (gibbon) 124
- Hymenoclea salsola* 92
- Hyperaspis pantherina* 416
- Hypochrysops halyetus* 478
- hypolimnion 135
- IBP 359
- ice 131
- Icerya purchasi* (cottony cushion scale insect) 415
- IGBP 359
- immigration to islands 341–2
- immobilization 369
- inbreeding, avoidance of 167–8
- inbreeding depression 465, 468, 472–3
- index of spatial heterogeneity 335
- Indian meal moth (*Plodia interpunctella*) 221
- ‘Indications of the spring’ 80
- indices of abundance 150–1, 285
- individual organisms 8, 34
- counting and estimating 147–8, 150–1
- identification 147, 148–9
- industrial melanism 48–50
- industry and habitat degradation 442–8, 453–4
- influenza viruses 22, 264
- infralittoral zone 138, 139
- inoculation biological control 416
- insects
- as agents of biological control 415–17
  - coevolution with plants 263, 351
  - fossil record 351
  - mouthparts 97
  - phytophagous 210
  - as pollinators 272, 273
- integrated farming systems 417–19, 421
- integrated pest management 417–19, 421
- intensive livestock management 428–9
- interference 103
- Intergovernmental Panel on Climate Change 93
- intermediate disturbance hypothesis 338
- International Biological Programme 359
- International Geosphere-Biosphere Programme 359
- intraspecific variation 41
- due to manmade selection pressures 48–50, 51
  - geographic 41–7, 48
- introduced species 17–21, 461–2
- invader species
- abandoned agricultural fields 24, 25
  - and competition for resources 184
  - dispersal 167, 168
  - economic cost 22, 23
  - introduced 17–21, 461–2
  - life history patterns 177
  - Mojave Desert 208–9
  - and species richness 352–3
- invertebrates
- carnivores 134
  - collector–filterers 133, 134
  - collector–gatherers 133, 134
  - grazer–scrapers 133, 134
  - lake communities 136
  - shredders 133, 134
  - stream communities 131–2, 133, 134
- IPCC 93
- IPM (integrated pest management) 417–19, 421
- Irena puella* (fairy bluebird) 124
- iron 91, 438
- oceans 136
  - sources 375
- irreplaceability analysis 476
- irrigation 420, 433
- islands
- biogeography 295, 340–5, 341–2, 355, 474–5
  - colonization 341–2, 344
  - evolution on 344–5
  - extinction on 341–2, 464
  - and metapopulation dynamics 295
  - and speciation 54, 55, 56
  - species–area relationships 340–5
- isolation
- and distribution 119
  - prezygotic 53
  - reproductive 52–3
- iteroparous species 152, 153, 155
- Juncus gerardi* 174
- Juncus squarrosus* 78
- Juniperus communis* 302
- juvenile phase 155
- K*-selecting habitats 177, 178, 179
- K* species 177, 178, 179, 180
- k*-value 287–91
- kakapo (*Strigops habroptilus*) 309
- kangaroo 98
- kelp 138
- key factor analysis 287–94
- key phase 290–1, 292
- keystone species 314–15, 318, 473
- kiwi 62, 63
- koala (*Phascolarctos cinereus*) 469, 470, 471
- laboratory experiments 10, 34
- laboratory systems, simple 10
- Labroides dimidiatus* 268, 269
- Lactobacillus sakei* 174
- Lagopus lagopus scoticus* (red grouse) 10, 222–3
- lake trout (*Salvelinus namaycush*) 136
- lakes 135–6, 137, 140
- carbon dioxide concentrations 94, 95
  - characteristics 117
  - cultural eutrophication 331, 379, 429–32
  - endorheic 378
  - energy flow pattern 368
  - nutrient availability 363–4
  - nutrient budgets 378
  - oligotrophic 379, 429
  - productivity 363–4, 365
  - saline 136, 378
  - species richness 347
  - stratification 117, 135–6
- lamp shells 213, 214
- land reclamation 448
- larch (*Larix*) 127
- Larrea mexicana* (creosote plant) 126, 208
- Larus argentatus* (herring gull) 53, 54
- Larus fuscus* (lesser black-backed gull) 53, 54
- Larus glaucescens* (glaucous-winged gull) 309–11
- Larus hyperboreus* (glaucous gull) 434
- Lasiommata maera* 76
- late potato blight (*Phytophthora infestans*) 283, 406
- Lates nilotica* (Nile perch) 462
- latitude
- and productivity 346, 360
  - and species richness 345–6
- lead 447–8
- leaf monkey (*Presbytis obscura*) 124
- leafing events and temperature 80, 81
- leaves
- composition 96
  - defenses 99, 100, 101
  - diversity in 85–6, 108
- Ledum palustre* 207
- legumes, nitrogen fixation 276–8, 376, 429
- Leichhardt’s grasshopper 97
- lemming (*Lemmus*) 128, 243
- Lemna* (duckweed) 148
- lemur 119
- leopard frog (*Rana pipiens*) 151
- Lepidodactylus lugubris* 184
- leprosy 458
- Leptaena richmondensis* 214
- Leptinotarsa decemlineata* (Colorado beetle) 73, 166–7, 288–91

- Lepus americanus* (snowshoe hare) 236–8  
*Lespedeza davurica* 303, 304  
 Lesser Antilles 343  
 lesser black-backed gull (*Larus fuscus*) 53, 54  
 lesser snow goose (*Chen caerulescens caerulescens*) 315  
 LIFE (low input farming and environment) 418  
 life cycles  
   annual 153–4  
   long-lived species 154–7  
   and reproduction 151–2, 179  
   staggered 206  
 life history  
   long-lived species 155  
   patterns 175–9, 180  
 life tables 157–62, 163, 179  
 light *see* solar radiation  
 lignin 97, 99, 369, 371  
 limestone 115  
 limpet 307, 308, 310–11  
 lindane 414  
*Linepithema humile* (Argentine ant) 437, 438  
 Linnaeus, Carolus 41  
*Liriodendron tulipifera* (yellow poplar) 115  
 LISA (low input sustainable agriculture) 418  
 lithosphere 375  
 littoral zone 136, 138, 139  
*Littorina littorea* (periwinkle snail) 247–8  
*Littorina obtusata* 223–4  
 live consumer system 359  
   energy flow through 366  
   relative role 367–9  
 lizards, neutral models of communities 212–13  
 llanos 125  
 locus 256  
 lodgepole pine 76  
 loess 408  
 logistic equation 172, 173–4, 190, 391, 393–4  
 logistic regression 156  
*Lolium multiflorum* 92  
 long-billed vulture (*Gyps indicus*) 30–3  
 long-term studies, need for 9  
*Lonicera japonica* 148  
 Lotka–Volterra interspecific competition model 189, 190–2  
 Lotka–Volterra predator–prey model 234, 235–6  
*Lottia digitalis* 310–11  
*Lottia pelta* 310–11  
*Lottia strigatella* 310–11  
 low input sustainable agriculture 418  
 lower input farming and environment 418  
 lumpers 119  
 Lyme disease 293–4  
*Lynx canadensis* (Canada lynx) 236–8  
*Macaranga* 204, 205  
 MacArthur and Wilson's equilibrium theory of island biogeography 295, 340–5, 341–2, 355, 474–5  
*Machilus thunbergii* 117, 118  
 magnesium 91  
   in lakes 137  
   sources 375  
 Malthus, Thomas 39, 65  
 mammals  
   dispersal 168  
   fossil record 351  
   marsupial 63, 64, 119, 351  
   placental 63, 64, 119  
   species richness 345  
 manatee (*Trichechus manatus*) 458  
 manganese 91, 438  
 manipulative field experiments 10, 24–6, 34  
 mantids 206  
*Mantis religiosa* 206  
 MAPSS biogeography model 129–30  
 marine bivalves, species richness 345  
 mark–recapture methods 150  
*Marmota bobac* 125  
*Marmota flaviventris* (yellow-bellied marmot) 159–61, 162  
 marsh tit (*Parus palustris*) 187  
*Marshallagia marshalli* 105  
 Marsham, Robert 80, 81  
 marsupial mammals 63, 64, 119, 351  
 mathematical models 10, 34  
   food webs 315–16  
   interspecific competition 189, 190–2  
   population crash 31–3  
   population growth 173–4  
   predator–prey 234, 235–6  
 matter flux 358, 374–9, 384  
 maximum sustainable yield 399–405, 420  
 mayfly 17–19  
 Mayr, Ernst 52  
 mean values 14–15  
 measles 240–1  
 megaherbivores, overexploitation 351–2, 460  
*Megalaima* (barbet) 124  
 melanism, industrial 48–50  
*Melanorhoea inappendiculata* 124  
*Melittaea cinxia* (Glanville fritillary butterfly) 296  
 meloxicam 33  
*Mercurialis annua* 92  
 mercury 447, 448  
 meta-analysis 214  
 metals, mining and extraction 446–8  
 metapopulations 243–5, 294–9, 321, 464–5  
 methane 129, 437, 444  
 methylmercury 448  
*Miconia* 122, 123  
 microbivores 370–1  
 microorganisms  
   in extreme environments 84  
   mutualistic role in digestion 273–4  
 microparasites  
   population dynamics 240–1  
   transmission threshold 240  
*Microtus apus* (swift) 284  
 microsatellites 56, 255, 256, 257, 258, 260, 261  
*Microtus canicaudus* (gray-tailed vole) 168  
 midlittoral zone 139  
 migration 9, 83, 127, 165–6, 168–9, 180, 294  
 milkweed 101  
 Millennium Ecosystem Assessment 391, 427  
 millipede 102  
 mimicry 102  
 mineral nutrients  
   aquatic environments 363–4  
   cycling 374–5  
   extraction by plants 91, 93  
   global biogeochemical cycles 382–3  
   immobilization 369  
   inputs 375–6  
   nutrient budgets 375–9  
   oceans 136–8  
   outputs 376–7  
   and productivity 362, 363–4  
   tropical rain forests 124  
 mineralization 369  
 minimum viable population 469, 481  
 mining 446–8  
   undersea 57  
 mistletoe (*Trilepidia adamsii*) 460  
 mitochondrial DNA 255, 257, 258, 260, 261  
 modular organisms 147, 148–9, 157, 179  
 modules 147  
 moi (*Polydactylus sexfilis*) 404  
 Mojave Desert, invader species 208–9  
 mole 102  
 molecular ecology 253–62  
 molecular markers 254–6, 279  
 monarch butterfly 101, 102  
 mongoose 197–8  
 monocultures 405–11, 420–1  
 monophagy 96  
 monophyletic radiation 56  
 monotremes 63  
 mountains 112, 113, 114  
 movement and population size 146

- MSY (maximum sustainable yield) 399–405, 420
- mtDNA 255, 257, 258, 260, 261
- multiple discriminant functions analysis 19
- Mus domesticus* (house mouse) 284, 285
- museums 38
- mussel 22, 23, 193–4, 244, 307, 332
- mutation 254–5
- mutual interference 241
- mutualism 51, 98, 252, 267–8, 279–80
- in agriculture 270–1
- ant–plant 269–70
- facultative 371
- in the gut 273–4
- mycorrhizas 274–6
- nitrogen fixation 276–8, 376, 429
- obligate 371
- protective 268–70
- and seed/pollen dispersal 271–3
- MVP (minimum viable population) 469, 481
- mycorrhizas 204, 206, 274–6
- Myristica gigantea* 124
- Mytilus californianus* 193–4, 310–11
- Mytilus californicus* 332
- myxoma virus/myxomatosis 264–6
- natal philopatry 256
- national parks 473–6
- Native Americans, tuberculosis 264
- natural experiments 24
- natural selection 37–41, 65–6, 414
- and coevolution 51
- and foraging behavior 229–33
- and genetic drift 254
- and genetic variation 466
- by pollution 48–50, 51
- by predation 46–7, 48, 49–50
- nature reserves 473–6
- near threatened species 459
- nectar 272–3
- nectaries 273
- negatively associated distribution 211, 213–14
- Nemoura avicularis* 371
- Nesameletus ornatus* 18
- net primary productivity 359, 360, 362, 363, 368
- net recruitment 174–5
- effects of exploitation 400–3
- neutral models 211–14
- New Zealand
- conservation of weta 306
- introduction of brown trout 17–21
- niche 106, 107, 108, 215
- breadth 326
- complementarity 202, 203, 204, 207, 215
- differentiation 187–9, 192–3, 199, 200, 202–4, 211, 212–13, 215
- dimensions 202
- fundamental 186
- overlap 326–7
- realized 186
- Nile delta, failure of silt deposition 411
- Nile perch (*Lates nilotica*) 462
- ninespine stickleback (*Pungitius pungitius*) 199
- nitric oxide 445
- nitrogen/nitrate 91
- allocation during plant life cycle 152
- availability in abandoned agricultural fields 24–6
- cultural eutrophication 331, 379, 429–32
- in drinking water 429
- and fertilizer use 420, 425
- fixation 276–8, 376, 429
- interaction with carbon dioxide 95
- as limiting resource 201, 206–7
- nitrogen cycle 381, 382
- in nutritional resources 97, 98–9
- oceans 136
- as pollutant 429
- and productivity 362
- sources 375–6
- uptake by arbuscular mycorrhizal fungi 275
- uptake by ectomycorrhizal fungi 275
- uptake by tundra plants 206–7
- nitrogenase 376
- nitrous oxide 129, 437
- Norfolk Island 56
- North Sea, variations in temperature over 65 million years 61
- northern coniferous forest 114, 119, 120, 127–8, 140
- food webs 237–8
- productivity 361, 363
- rainfall and temperature 115
- northern white cedar (*Thuja occidentalis*) 115
- NPP (net primary productivity) 359, 360, 362, 363, 368
- nuclear power 438–40
- null hypothesis 12, 13, 211–14
- nutrient budgets
- aquatic communities 376, 378–9
- terrestrial ecosystems 375–7
- nutrients *see* mineral nutrients
- oak (*Quercus robur*) 58, 59, 149
- Obelia* 148
- observation 10
- oceans 136–8, 140–1
- cultural eutrophication 331, 379, 430–2
- currents and climatic patterns 112, 113
- dead zones 379, 430
- energy flow pattern 368
- nutrient availability 364
- nutrient budgets 378–9
- patterns in conditions and resources 116–17
- productivity 360, 363, 364, 365
- species richness 347–8
- trophic structure 369
- Ochotona princeps* (American pika) 296–7
- On the Origin of Species by Means of Natural Selection* (Darwin) 39, 41, 51
- Oncorhynchus* 155–6, 259
- Oncorhynchus kisutch* (coho salmon) 259
- Oncorhynchus mykiss* (steelhead trout) 104
- Oncorhynchus nerka* (sockeye salmon) 259
- Oniscus asellus* 374
- opossum 102
- optimal diet width 231–2
- optimal foraging theory 229–33, 249
- orange-crowned warbler (*Vermivora celata*) 187–8
- order from strength scenario 451, 452
- organochlorine insecticides 433, 434
- oriental white-backed vulture (*Gyps bengalensis*) 30–3
- Orthezia insignis* 415–16
- Oryctolagus cuniculus* *see* rabbit
- ostrich (*Struthio camelus*) 62, 63
- overcollection 460
- overexploitation 460
- fisheries 399–405, 420
- and the fossil record 351–2
- ox 246–7
- oxygen
- in aquatic environments 130–1
- in streams and rivers 131
- oystercatcher (*Haematopus bachmani*) 309–11
- ozone 129, 437
- ozone layer 444–6
- P*-values 12, 13, 34
- quoting 13–14
- Pacific salmon (*Oncorhynchus*) 155–6, 259
- Palaemonetes pugio* 82, 83
- Palaemonetes vulgaris* 82, 83
- pampas 125
- Panama disease 407
- pandemic 264
- Pangaea 350
- Papua New Guinea 343, 344
- Paracantha culta* 417
- paradox of enrichment 325, 331



- parasites 95, 249, 279  
   coevolution with hosts 264–6, 267  
   compensation and defense responses to 223–5  
   competition between 222, 242  
   effects on fitness and abundance of hosts 220–1  
   interacting factors adding to effects 222–3  
   population dynamics 240–1  
   as predators 218–19  
   and symbiosis 268  
   transmission 228, 229  
   transmission threshold 240  
 parasitoid wasp 219, 221  
 parasitoids 219  
*Parasponia* 276  
*Parus ater* (coal tit) 187, 246  
*Parus caeruleus* (blue tit) 187  
*Parus cristatus* (crested tit) 246  
*Parus major* (great tit) 154–5, 156, 166, 187  
*Parus montanus* (willow tit) 187, 246  
*Parus palustris* (marsh tit) 187  
*Paspalum* 277–8  
*Pasteuria ramosa* 105  
 patch dynamics 299  
 patches/patchiness 116, 119, 122  
   and community structure 299–301  
   and interspecific competition 193–5, 196, 215  
   and metapopulation dynamics 294–9  
   and population dynamics 294, 321  
   and predation 230, 243–5  
   and succession 306–7, 308  
   temperate forests 127  
 PCBs (polychlorinated biphenyls) 434  
 PCR (polymerase chain reaction) 255  
 PE (production efficiency) 366, 367  
 peat bogs 116, 127  
 penguin 71  
 peppered moth (*Biston betularia*) 49–50  
 peregrine falcon (*Falco peregrinus*) 425, 460  
 perennial plants 151  
   in abandoned agricultural fields 24, 25  
 periwinkle snail (*Littorina littorea*) 247–8  
 permafrost 128  
 Permian decline 350  
 pertussis 241  
 Peruvian anchovy (*Engraulis ringens*) 137, 402, 403  
 pest control 412–17, 421  
 pesticides 6, 413–15, 424–5  
   and biodiversity 461  
   in integrated pest management 417, 421  
   organochlorine 433, 434  
   as pollutants 413, 425–6, 432–3, 434  
   projected increase in use 420  
 pests  
   biological control 6, 415–17, 457–8  
   definition 412  
   economic injury levels 412–13, 417  
   economic threshold 413  
   equilibrium abundance 412  
   evolution of resistance 414  
   integrated pest management 417–19  
   population fluctuations 412  
   potential 412, 413  
   secondary 413–14  
   target pest resurgence 413  
 PET (potential evapotranspiration) and species richness 328–9  
 pH 71  
   extremes of 84, 336  
   and niche dimensions 106, 107  
   rainwater 438  
   streams 132  
 phage 266, 267  
*Phascolarctos cinereus* (koala) 469, 470, 471  
*Pheidole* 311, 312  
 phenology 80  
*Phlox drummondii* 158, 159, 160–1, 162  
*Phoeniconaias minor* 378  
*Phoenicopterus roseus* 136  
 phosphorus/phosphate 91, 187  
   cultural eutrophication 331, 429–32  
   as limiting resource 201  
   oceans 136  
   phosphorus cycle 381, 382  
   and productivity 362, 363  
   projected increases due to agriculture 420  
   sources 375  
   uptake by arbuscular mycorrhizal fungi 275–6  
 photoperiod 75–6, 154  
 photosynthesis  
   C3 pathway 90, 95, 108  
   C4 pathway 90, 95, 108  
   CAM 90, 108  
   and carbon dioxide 94–5  
   in early- and late-successional plants 304  
   gross primary productivity 358  
   as limiting factor in human population growth 398  
   at low radiation intensity 107  
   need for water 88–9, 90  
   photoinhibition 85  
   response to changes in solar radiation 85, 108  
   in sun/shade plants 87, 88  
   in tropical rain forest 122  
 photosynthetic efficiency 361  
*Phthorimaea operculella* (potato tuber moth) 418  
*Physella gyrina* 313  
 phytoaccumulation 448  
 phytophagous insects, interspecific competition in 210  
*Phytophthora infestans* (late potato blight) 283, 406  
 phytoplankton 136  
   and eutrophication 331, 432  
   limiting resources and diversity regulation in communities 200–2  
   productivity 363, 368  
   species richness 330, 331, 338–9  
 phytoremediation 448  
*Phytoseiulus persimilis* 416  
 phytostabilization 448  
 phytotransformation 448  
*Picea* 58, 59, 127, 128  
*Picea critchfeldii* 60  
 pied flycatcher (*Ficedula hypoleuca*) 220–1  
*Pieris rapae* 101, 224–5  
 pig, feral 284  
 pigmy owl (*Glaucidium passerinum*) 246  
 pike (*Esox lucius*) 131, 430, 431  
 pikeminnow (*Ptychocheilus lucius*) 434–5  
 pine savanna 125  
 pink pigeon (*Columba mayeri*) 472–3  
*Pinus* 127  
*Pinus ponderosa* (ponderosa pine) 377  
*Pinus resinosa* 204, 303  
*Pinus strobes* (eastern white pine) 118, 303  
*Piper cenocladum* 311, 312  
*Pisaster ochraceus* 332  
 placental mammals 63, 64  
 plant collectors 38, 460  
 plants  
   as animal food resource 96–9  
   ‘belly’ 126  
   coevolution with insects 263, 351  
   compensatory responses to herbivory 223–5, 262–3, 313  
   composition 96–7  
   defenses 99–101, 126, 223–4, 262–3, 313  
   desert 89–90, 92, 126  
   detritus 371–3  
   differing evolutionary rates 340  
   early-/late-successional 304, 305  
   fossil record 350–1  
   lakes 136  
   in land reclamation 448  
   metapopulations 298–9  
   mutualisms with ants 269–70  
   resources 108  
     carbon dioxide 92–5  
     mineral nutrients 91, 93  
     solar radiation 85–8  
     water 88–91, 92  
   sun/shade 86–8



- Platanthera* 273  
*Plebejus argus* (silver-studded blue butterfly) 294, 298  
*Plectonema nostocorum* 84  
*Plectroglyphidodon lacrymatus* 299–300  
*Plodia interpunctella* (Indian meal moth) 221  
*Poa annua* 195, 196  
*Poecilia reticulata* (guppy) 46–7, 48  
polar bear 83, 477  
polar cod (*Boreogadus saida*) 434  
*Pollicipes polymerus* (goose barnacle) 310–11  
pollination  
  and habitat degradation 433  
  mutualism in 272–3  
  as provisioning ecosystem service 458  
pollution 424–6  
  atmospheric 436–8, 439  
  and biodiversity 461  
  cultural eutrophication 331, 379, 429–32, 443  
  due to agriculture 331, 379, 413, 425–6, 428–33, 453  
  due to power generation 435–41  
  ecology of 6  
  economics of 427–8  
  and fertilizer use 426, 429  
  natural selection due to 48–50, 51  
  and pesticide use 413, 425–6, 432–3, 434  
  in urban and industrial landscapes 442–8  
polychlorinated biphenyls 434  
*Polydactylus sexfilis* (moi) 404  
polymerase chain reaction 255  
polyphagy 96  
*Pomacentrus wardi* 299–300  
ponderosa pine (*Pinus ponderosa*) 377  
population crash 30–3  
population cycles 128  
  and predation 233–9  
population dynamics 282–3  
  determinants 283–94, 320–1  
  and exploitation of resources 400–5  
  idealized diagrams 288  
  key factor analysis 287–94  
  parasites 240–1  
  and patches/patchiness 294, 321  
  and predation 233–45, 249  
  role of dispersal and migration 294  
population ecology 40  
population growth rate 30  
population projection matrices 471  
population viability analysis 468, 469–72, 481  
populations 8, 34, 179  
  definition 146  
  determination 285–7  
  divergence 41–7, 48  
  effective population size 466  
  exponential growth 172, 173–4  
  factors affecting size 146–7  
  growth patterns 171–5  
  growth rate and food availability 283, 284  
  impact of interspecific competition 173–4  
  impact of intraspecific competition 169–75, 173–5, 180  
  and individuals 147, 148–9, 179  
  intrinsic rate of natural increase 172, 173  
  logistic (sigmoidal/S-shaped) growth 172, 173–4  
  measurement  
    limitations of 283  
    methods 147–8, 150–1, 179  
  minimum viable population 469, 481  
  regulation 285–7  
  small  
    demographic risks 463–5, 480  
    genetic problems 465–6, 467, 480  
  stability 284, 285  
    and food webs 313–20  
  see also metapopulations  
*Populus* 127  
*Populus deltoides* × *nigra* 448  
*Porcellio scaber* 374  
*Posidonia* 139  
*Postelsia palmaeformis* (sea palm) 193–4  
potassium 91, 375  
potato, late blight 283, 406  
potato tuber moth (*Phthorimaea operculella*) 418  
potential evapotranspiration and species richness 328–9  
power generation 435–41, 453  
prairie 125  
prairie dog 102  
predation 96  
  and coevolution 262–6, 267  
  and community structure 246–8, 249  
  and crowding 241–3  
  effects on prey populations 225–8  
  interacting factors affecting 222–3, 249  
  by invading species 19–20, 21  
  natural selection by 46–7, 48, 49–50  
  and patches/patchiness 230, 243–5  
  population dynamics 233–45, 249  
  predator behavior 228–33, 249  
  prey compensation and defense 223–5  
  prey fitness and abundance 220–1  
  selective 247  
  and species richness 327, 331–4, 354  
  in tropical communities 345–6  
predator-mediated coexistence 246, 331–4  
predators 95, 96  
  behavior 228–33, 249  
  classification 218–19  
  coevolution with prey 262–6, 267  
  competition between 241–3  
  definition 218, 249  
  diet width 231–2  
  effects of crowding 241–3  
  effects of pesticides 433, 434  
  foraging 228–33, 249  
  generalist 231–2, 249, 262  
  as keystone species 315  
  Lotka–Volterra predator–prey model 234, 235–6  
  mutual interference 241  
  in patches 230, 243–5  
  pattern of contact with prey 228, 229  
  population cycles 233–9  
  ‘sit and wait’ 228, 229  
  specialist 231–2, 249, 262  
  and trophic cascades 309–12  
  ‘true’ 218, 219, 249  
predictive studies 7  
pregnancy 152  
*Presbytis obscura* (leaf monkey) 124  
prey  
  coevolution with predators 262–6, 267  
  compensation and defense 223–5  
  effects of crowding 242–3  
  fitness and abundance 220–1  
  Lotka–Volterra predator–prey model 234, 235–6  
  in patches 230, 243–5  
  population cycles 233–9  
  populations 225–8  
*Primula* 100  
probabilities 12–14, 34  
production efficiency 366, 367  
productivity  
  and biodiversity 372  
  and global climate change 359  
  gross primary 358, 363  
  and latitude 346, 360  
  net primary 359, 360, 362, 363, 368  
  primary  
    definition 358  
    fate of 364–9, 383  
    geographic patterns 360, 383  
    limiting factors 360–4  
    relationship with secondary productivity 364–5, 366  
  secondary 359, 368  
    relationship with primary productivity 364–5, 366  
  and species richness 328–31, 354  
progeny, trade-off between number and fitness 177, 178  
*Promerops cafer* (Cape sugarbird) 272

- pronghorn antelope (*Antilocapra americana*) 125, 126
- Protea* 476
- Protea eximia* 272
- protists 73, 74
- Protonemura meyeri* 371
- provisioning ecosystem services 427, 428, 433, 458
- proximate explanations 7
- Prunus speciosa* 118
- Pseudomonas fluorescens* 199, 200, 266, 267
- Pseudomyrmex concolor* 270
- Pseudomyrmex ferruginea* 269–70
- Pseudotsuga menziesii* (Douglas fir) 176, 226, 227, 335
- Pteropus* (flying fox) 465
- Ptychocheilus lucius* (pikeminnow) 434–5
- Pungitius pungitius* (ninespine stickleback) 199
- pure ecology 5, 34
- PVA (population viability analysis) 468, 469–72, 481
- Pyrodictium occultum* 74
- Quercus robur* (oak) 58, 59, 149
- Quercus rubra* (red oak) 127
- r*-selecting habitats 177, 178, 179
- r* species 177, 178, 179, 180
- rabbit 98, 102
- myxomatosis 264–6
- population control 146
- radiation 438–40
- Rafinesquina alternata* 214
- ragwort (*Senecio*) 96, 176
- rain shadow 112, 113
- rainfall
- and altitude 347
- biome ranges 115
- desert 126, 153–4
- and global climate change 476–9
- global patterns 111–13
- and productivity 361–2
- savanna 115, 125
- and species richness 329–30
- tropical rain forest 115, 122
- rainwater
- chemical composition 376
- see also acid rain
- RAMAS-STAGE 471
- Rana pipiens* (leopard frog) 151
- Rana sylvatica* (wood frog) 291, 292
- random sampling 15–16, 16
- Rangifer tarandus* 128
- rank–abundance diagrams 325–6
- Ranunculus bulbosus* 273
- Ranunculus ficaria* 273
- Raphanus sativus* (wild radish) 101, 224–5
- rare species 459–60, 480
- raspberry 272
- rat 22, 242
- Ratufa affinis* 124
- Ratufa bicolor* 124
- RDZs (resource depletion zones) 90, 91, 104
- reciprocal transplant experiments 42, 44–6
- recruitment and population dynamics 288
- red brome 208–9
- red fire ant (*Solenopsis invicta*) 22, 23
- red grouse (*Lagopus lagopus scoticus*) 10, 222–3
- red kangaroo 284
- red oak (*Quercus rubra*) 127
- red squirrel 83
- red wolf (*Canis rufus*) 260, 261, 262
- regression coefficient 290
- regulating ecosystem services 427, 458
- reindeer 128
- replacement cost 428
- replacement series 277
- representative samples 11, 15
- estimation from 150
- reproduction
- in annual species 153–5
- cost of 151–2, 175, 176
- early 176–7
- and life cycles 151–2, 179
- in long-lived species 154–7
- and photoperiod 154
- relationship with age and size 156, 157
- resilience 314
- resistance 314
- resource depletion zones 90, 91, 104
- resource use overlap 212
- resources 107, 108
- for animals 95–103, 108
- differential utilization 187–9, 192–3, 202–3, 212–13, 215
- distinction from conditions 70
- effect of intraspecific competition on 103–6
- effect of species spatial separation on utilization 204, 205, 206
- effect of species temporal separation on utilization 206–7
- human harvesting from the wild 399–405
- limiting 183–4, 200–2, 203, 206–7
- and migration 168–9
- patterns
- aquatic environments 116–17
- large-scale 111–13
- small-scale 113–16
- temporal 117, 118
- for plants 85–95, 108
- and regulation of diversity 200–2
- richness, and species richness 328–31
- uneven distribution among human population 393
- respiratory heat 358, 365, 366, 368
- restoration ecology 333–4, 448–51, 452, 454
- restriction fragment length polymorphism (RFLP) 256, 259, 260, 261
- rhea (*Rhea americana*) 62, 63
- Rhinanthus minor* 333, 334
- Rhinocyllus conicus* 417
- rhizobia 276–8
- Rhododendron* 115
- Rhododendron lapponicum* 156
- Rhodoglossum affine* 338
- riparian vegetation 133
- rivers see streams and rivers
- rodents, species richness 329–30
- Rodolia cardinalis* 415
- root hairs 90, 91, 108
- roots
- mineral nutrient uptake 91, 93, 108
- systems 90–1, 92, 93, 108
- water uptake 90–1, 92, 108
- rose aphid 97
- rose periwinkle (*Catharanthus roseus*) 458
- roundworm (*Ascaris*) 39
- royal catchfly (*Silene regia*) 471–2
- rumen 98
- rush 78, 174
- rush moth (*Coleophora alticolella*) 78
- Sagina procumbens* 92
- saguaro cactus 74–5
- Sahara mustard 208–9
- saiga antelope (*Saiga tatarica*) 125
- St Helena gumwood (*Commidendrum robustum*) 415–16
- Salazaria mexicana* 92
- Salicornia* 222
- salinity
- estuaries 139
- lakes 136
- and niche dimensions 106, 107
- responses to 82, 83
- salinization 410
- Salix alba* (tropical willow) 458
- Salix cinerea* (willow) 174
- Salix cordata* (sand-dune willow) 220
- Salix herbacea* (dwarf willow) 344
- Salmo trutta* (brown trout) 17–21, 18, 34, 131
- salmon 232, 233
- salt marsh, competition and parasitism in 222
- Salvelinus leucomaenis* (white-spotted charr) 78, 80, 184–6

- Salvelinus malma* (Dolly Varden charr) 78, 80, 184–6
- Salvelinus namaycush* (lake trout) 136
- Salvia dorrii* 92
- Salvinia molesta* 221
- sampling 11, 15
- sand-dune willow (*Salix cordata*) 220
- sand dunes 10, 302, 303
- sand shrimp (*Crangon septemspinosa*) 107
- Sander vitreus* 136
- sandwich tern (*Sterna sandvicensis*) 441
- Santiria laevigata* 124
- sapphire rockcress (*Arabis fecunda*) 42–3
- savanna 114, 119, 120, 125, 140
- rainfall and temperature 115, 125
- water deficit 89
- Saxifraga bronchialis* (spotted saxifrage) 149
- scale 8–9, 34, 111
- and interspecific competition 186
- and patchiness 116
- and patterns in conditions and resources 111–16
- scavengers 374
- human 442
- SCFAs (short-chain fatty acids) 274
- schistosomiasis 411
- Schizachyrium scoparium* 302, 303
- scientific rigor 11, 34
- sea anemones 45, 202, 203
- sea grasses 139
- sea otter 171–2
- sea palm (*Postelsia palmaeformis*) 193–4
- sea slug 39
- seashore *see* coastal environments
- seasonal cycles 78, 80, 81
- annual species 153
- long-lived species 154
- and migration 168–9
- in productivity 362, 363
- recording 80, 81
- savanna 125
- and species richness 337
- temperate forest 127
- temperature extremes 83
- seaweed 138, 223–4
- Sebastes melanops* (black rockfish) 405
- seed bank 153, 164, 299
- seed rain 153
- seeds
- composition 96, 97
- dispersal 271–2
- dormancy 153–4
- germination 75–6
- self-shading 88
- semelparous species 152, 153, 155
- Senecio* (ragwort) 96, 176
- Seraria viridis* 303
- sewage disposal 442–4
- shade leaves 86
- Shannon (Shannon–Weaver) diversity index 325, 339
- sharks 460
- sheep 98
- Sheep Range, Nevada 59
- Shen Nung 38
- short-chain fatty acids 274
- shredders 371–2
- significance testing 12, 13
- Silene regia* (royal catchfly) 471–2
- silicon/silicate 103, 137, 183–4, 187, 201
- silver birch (*Betula pendula*) 169, 170
- silver-spotted skipper butterfly (*Hesperia comma*) 297
- silver-studded blue butterfly (*Plebejus argus*) 294, 298
- simple laboratory systems 10
- Simpson's index 200–1
- Simulium vittatum* (blackfly) 168
- size as predictor of fecundity 156, 157
- skin cancer 444
- slug 100
- small watershed technique 27
- snail 102, 223–4
- snowshoe hare (*Lepus americanus*) 236–8
- sociopolitical scenarios in ecosystem
- service maintenance and restoration 450–1, 452
- sockeye salmon (*Oncorhynchus nerka*) 259
- soil 114
- acidic 115
- calcareous 115
- conservation strategies 409–10
- degradation and erosion due to
- agriculture 407–10, 421, 424
- disturbance, germination following 153
- temperate forests 127
- tropical rain forests 124
- water retention 90
- solar radiation 85–8, 108
- cycles 85, 86
- dependence on Earth's tilt and rotation 111, 112
- human exposure to 444
- as limiting resource 201
- oceans 136
- and productivity 360, 361
- tropical rain forest 122
- variations in 85, 86
- Solenopsis invicta* (red fire ant) 22, 23
- South Africa, Cape Floristic Region 476
- southern corn leaf blight (*Helminthosporium maydis*) 406
- soybean (*Glycine soja*) 277–8
- Sparaxis grandiflora* 151–2
- sparrow hawk (*Accipiter nisus*) 425, 426
- Spartina* 139
- spatial distribution patterns 164–5
- aggregated 165, 194–5, 196
- effects of dispersal and migration 165–6
- and interspecific competition 184–6, 204, 205, 206
- and isolation 119
- large-scale 111–13
- random 165
- regular 165
- small-scale 111–13
- spatial heterogeneity and species richness 334–5, 354
- spatial patterns 164–5
- spatial scales 8
- speciation 66, 256–62
- allopatric 53
- ecology of 51–7
- and islands 54, 55, 56
- orthodox 52–3
- sympatric 53
- species
- classification of threat to 459
- definitions 52
- differentiation between 260–2, 279
- differentiation within 256–9, 279
- endemic 56
- estimates of total number 456, 457
- evolution within 41–51
- geographic variation within 41–7, 48
- of least concern 459
- rare 459–60, 480
- variation within due to manmade selection 48–50, 51
- species–area relationships 340–5
- species richness 324–6, 456
- and altitude/depth 346–8
- appraisal of patterns 352–3
- cascade effects 348–9
- and climatic variation 337–8, 354
- and disturbance 338–9, 354–5
- and environmental harshness 335–6, 354
- and evolutionary equilibrium 339, 355
- fossil record 349–52, 355
- gradients 340–9, 355
- and habitat area 340–5, 355
- hotspots 474
- and interspecific competition 327
- latitudinal patterns 345–6
- model 326–7, 354
- and predation 327, 331–4, 354
- and productivity 328–31, 354
- and rate of evolution 340
- and resource richness 328–31
- and spatial heterogeneity 334–5, 354
- spatially varying factors in 328–37
- and succession 348–9
- temporally varying factors 337–40
- see also* biodiversity

- Spencer, Herbert 40  
*Spergula arvensis* 153  
*Spermophilus citellus* (European ground squirrel) 82  
 splitters 119  
 spores 84, 153–4  
 spotted alfalfa aphid (*Therioaphis trifolii*) 413  
 spotted saxifrage (*Saxifraga bronchialis*) 149  
 spruce budworm (*Choristoneura fumiferana*) 128  
 spruce (*Picea*) 58, 59, 127, 128  
 stability 314  
 standard errors 14–15  
 standing crop 358  
 starfish 244  
 static life table 157–8, 162, 163  
 statistics 11–16, 34  
 steelhead trout (*Oncorhynchus mykiss*) 104  
*Stellaria media* 195, 196  
 steppes 125  
*Sterculia parviflora* 124  
*Sterna sandvicensis* (sandwich tern) 441  
*Stichodactyla mertensii* 203  
*Stipa bungeana* 303  
*Stizostedion vitreum* 430, 431  
 stoloniferous organisms 149  
 stoneflies 371–2  
 stratified random sampling 15–16  
 strawberry (*Fragaria*) 149  
 streams and rivers 131–5, 140  
   catchment area management 449–50, 451  
   consequences of human activities 133, 134–5  
   damming 410–11  
   disturbances in 132–3, 338–9  
   energy flow pattern 368, 369  
   role in nutrient budgets 376, 377, 378  
   water abstraction 433–5  
*Strigops habroptilus* (kakapo) 309  
*Strombidinopsis multiauris* 73  
*Strongyloides ratti* 242  
*Strophomena planumbona* 214  
 strophomenide brachiopods 213, 214  
*Struthio camelus* (ostrich) 62, 63  
 suberin 369  
 subpopulations 295–8, 463, 464–5  
 subspecies 53  
 succession 8–9, 34, 301–7, 308  
   animals in 305  
   chronosequence 302  
   on cooled volcanic lava 117, 118  
   dominance-controlled communities 301  
   early and late species 302, 304, 305  
   idealized 301  
   manipulation 306  
   old-field 23–6, 34, 302, 303, 304  
   and patches/patchiness 306–7, 308  
   primary 301–2  
   secondary 302  
   and species richness 348–9  
 sugar maple (*Acer saccharum*) 127  
 sulfur 91  
   sulfur cycle 381, 382  
 sulfuric acid 101  
 sun leaves 86  
 sunbird (*Arachnothera*) 124  
 supporting ecosystem services 427  
 supralittoral zone 139  
 Surtsey 344  
 survival and predation 220–1  
 survival of the fittest 40  
 survival plans 473  
 survivorship curves 161, 162, 163–4, 179  
 sustainability 389–91  
   and agriculture 405–21  
   and economics 412–13  
   of fisheries 399–405  
   and human population growth 391–9, 420  
   and integrated farming systems 417–19, 421  
   of monocultures 405–11, 420–1  
   and pest control 412–17, 421  
   triple bottom-line approach 448–51, 452  
   of water as resource 410–11  
 sustainable biosphere initiative 390  
 swallow (*Hirundo rustica*) 169  
 swallowtail butterflies 345  
 swift (*Micropus apus*) 284  
*Sylvilagus brasiliensis* 264–5  
 symbiosis 268  
 sympatric species 199  
 synchronous flowering 157  
*Synedra ulna* 183–4, 186  
 systematics 38  
*Tachigali myrmecophila* 270  
*Taeniopteryx nebulosa* 371  
 taiga *see* northern coniferous forest  
 Tansley, A.G. 4, 5  
 target pest resurgence 413  
*Tarsobaenus* 311, 312  
 taxon richness patterns, fossil record 349–52, 355  
 taxonomy 38  
 technogarden scenario 451, 452  
*Tectus niloticus* (trochus) 405  
 temperate deciduous forest 114, 119, 120, 126–7, 140  
   productivity 361  
   rainfall and temperature 115  
 temperate grassland 114, 119, 121, 125–6, 140  
 temperature  
   and acclimatization 76–7, 81  
   biome ranges 115  
   and competition 78, 80  
   desert 126  
   effects of altitude and latitude 114, 116  
   effects on interactions between organisms 78  
   extremes of 74–5, 107–8, 335  
   seasonal 83  
   and global climate change 93, 437, 476–9  
   lakes 117, 135–6  
   and leafing events 80, 81  
   and niche dimensions 106, 107  
   North Sea over 65 million years 61  
   and productivity 360, 361–2  
   responses to 72, 73, 74–5, 81–3, 84, 107–8  
   streams 132  
   variation with glacial cycles 58, 59  
 temporal separation and resource utilization 206–7  
*Tenodera sinensis* 206  
 termite, gut flora 8, 9  
*Tetranychus urticae* 416  
*Thalassarche chrysostoma* (grey-headed albatross) 256, 257, 258  
*Thalassarche impavida* (black-browed albatross) 256, 257, 258  
*Thalassarche melanophris* (black-browed albatross) 256, 257, 258  
*Therioaphis trifolii* (spotted alfalfa aphid) 413  
 thermocline 135  
 thermophiles 74, 84, 138  
*Thiobacillus ferrooxidans* 84  
*Thlaspi caerulescens* 448  
*Thomomys bottae* (gopher) 125  
 Thomson's gazelle 227, 228  
 threshold population size 240  
 thrush (*Turdus*) 426  
*Thuja occidentalis* (northern white cedar) 115  
 thymine 254, 256  
 tides 138  
*Tidestromia oblongifolia* (desert honeysweet) 89–90  
 time delays 234  
 time scales 8–9, 34  
 tinamou 62, 63  
 tolerators 89  
 topography, effect on climate 112, 113, 114  
 toxaphene 414  
 trade-offs  
   between growth and reproduction 151–2, 175, 176  
   between progeny number and fitness 177, 178

- Tradescant, John Jr 38  
 Tradescant, John Sr 38  
 transhumance 168–9  
 transpiration 89–90  
 travel cost 428  
 ‘treatment’ wetlands 432  
 trees  
   as *K* species 177, 178, 179  
   spatial separation 204, 205  
   species richness  
     and latitude 345  
     in relation to potential  
       evapotranspiration 328–9  
*Trialeurodes vaporariorum* (whitefly) 416  
*Trichechus manatus* (manatee) 458  
 trichomes 99, 100  
*Trichostrongylus tenuis* 223  
*Trifolium repens* (white clover) 45–6, 100  
*Trilepidia adamsii* (mistletoe) 460  
 trochus (*Tectus niloticus*) 405  
 trophic cascade 309–12  
 trophic levels 364  
   and energy flux 364–5, 366  
   trophic transfer efficiency 367  
 tropical rain forest 114, 119, 121, 122–5,  
   140  
   rainfall and temperature 115, 122  
 tropical seasonal forest 114  
 tropical willow (*Salix alba*) 458  
*Trypanosoma* 220–1  
*Tsuga canadensis* (eastern hemlock) 115  
*Tuberculatus quercicola* 271  
 tuberculosis 264  
*Tubularia crocea* 149  
 tundra 114, 119, 121, 127–8  
   nitrogen uptake by plants 206–7  
   rainfall and temperature 115  
*Turbinaria reniformis* 149  
*Turdus* (thrush) 426  
*Tympanuchus cupido cupido* (heath hen)  
   463  
*Tympanuchus cupido pinnatus* (greater  
   prairie chicken) 466  
*Typhlodromus occidentalis* 243–4  
  
*Ulex europaeus* (gorse) 306  
 ultimate explanations 7  
  
*Ulva* 338  
 unitary organisms 147  
 United States  
   ‘dust bowl’ disaster 408  
   invading species 22, 23  
 urbanization and habitat degradation  
   442–8, 453–4  
*Ursus americanus* (black bear) 232, 233  
*Ursus arctos* (brown bear) 232, 233  
  
*Vaccinium vitis-idaea* (cranberry) 207  
*Venturia canescens* 221  
*Vermivora celata* (orange-crowned  
   warbler) 187–8  
*Vermivora virginiae* (Virginia’s warbler)  
   187–8  
*Vestiges of Creation, The* 38  
 viceroy butterfly 102  
*Vipera aspis* (aspic viper) 176  
 Virginia’s warbler (*Vermivora virginiae*)  
   187–8  
 vole 168, 243  
 VORTEX 469, 470  
 vulnerable species 459  
*Vulpia ciliata* ssp. *ambigua* 275–6  
*Vulpia fasciculata* 104, 105  
 vultures 30–3, 35  
  
 Wallace, Alfred Russel 37–41, 39, 65  
 walleye 136, 430, 431  
 Walnut Creek 449–50, 451  
 wasp, parasitoid 219, 221  
 water  
   abstraction from watercourses 433–5  
   availability 411  
   hydrological cycle 380–1  
   as plant resource 88–91, 92, 108  
   pollution 411, 429, 461  
   shortage  
     plant responses to 88–90, 108  
     and productivity 361–2  
   soil reserves 90–1, 92  
   structure and properties 130–1  
   sustainability as resource 410–11, 424  
 watermelon (*Citrullus lanatus*) 433  
 weather, and population regulation 287  
 weta (*Deinacrida mahoenuiensis*) 306  
  
 wetfall 376  
 wetlands, ‘treatment’ 432  
 wheat, pests of 416  
 White, Gilbert 284  
 white clover (*Trifolium repens*) 45–6, 100  
 white-spotted charr (*Salvelinus  
   leucomaenis*) 78, 80, 184–6  
 whitefly (*Trialeurodes vaporariorum*) 416  
 whooping cough 241  
 wild radish (*Raphanus sativus*) 101,  
   224–5  
 wildebeest (*Connochaetes taurinus*) 125,  
   284  
 willow (*Salix cinerea*) 174  
 willow tit (*Parus montanus*) 187, 246  
 wilting 88, 90  
 wind power 440–1  
 Wisconsin Lake District 137  
 wolf 83  
   gray wolf (*Canis lupus*) 260, 261  
   red wolf (*Canis rufus*) 260, 261, 262  
 wolverine 83  
 wood frog (*Rana sylvatica*) 291, 292  
 woodlice 374  
 wormwood 126  
 Wu Hou observations 80  
  
*Xylopia stenopetala* 124  
  
 yellow-bellied marmot (*Marmota  
   flaviventris*) 159–61, 162  
 yellow poplar (*Liriodendron tulipifera*)  
   115  
 yellow star thistle (*Centaurea solstitialis*)  
   22, 23  
  
 zebra 98, 125  
 zebra mussel (*Dreissena polymorpha*) 22,  
   23  
 zebu 246–7  
 zero isoclines 190, 191, 235–5–6  
 zinc 91  
   tolerance to 51  
 zonation, coastal 138–9  
 zooplankton 430, 431  
 zoos 38  
*Zostera* 139